T3: INTERVENTION TECHNICAL SUMMARY

A report provided to the Australian Government by the Reef Restoration and Adaptation Program

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1. PREAMBLE

The Great Barrier Reef

Visible from outer space, the Great Barrier Reef is the world's largest living structure and one of the seven natural wonders of the world, with more than 600 coral species and 1600 types of fish. The Reef is of deep cultural value and an important part of Australia's national identity. It underpins industries such as tourism and fishing, contributing more than $6B a year to the economy and supporting an estimated 64,000 jobs.

Why does the Reef need help?

Despite being one of the best-managed coral reef ecosystems in the world, there is broad scientific consensus that the long-term survival of the Great Barrier Reef is under threat from climate change. This includes increasing sea temperatures leading to coral bleaching, ocean acidification and increasingly frequent and severe weather events. In addition to strong global action to reduce carbon emissions and continued management of local pressures, bold action is needed. Important decisions need to be made about priorities and acceptable risk. Resulting actions must be understood and co-designed by Traditional Owners, Reef stakeholders and the broader community.

What is the Reef Restoration and Adaptation Program?

The Reef Restoration and Adaptation Program (RRAP) is a collaboration of Australia's leading experts aiming to create a suite of innovative and targeted measures to help preserve and restore the Great Barrier Reef. These interventions must have strong potential for positive impact, be socially and culturally acceptable, ecologically sound, ethical and financially responsible. They would be implemented if, when and where it is decided action is needed and only after rigorous assessment and testing.

RRAP is the largest, most comprehensive program of its type in the world; a collaboration of leading experts in reef ecology, water and land management, engineering, innovation and social sciences, drawing on the full breadth of Australian expertise and that from around the world. It aims to strike a balance between minimising risk and maximising opportunity to save Reef species and values.

RRAP is working with Traditional Owners and groups with a stake in the Reef as well as the general public to discuss why these actions are needed and to better understand how these groups see the risks and benefits of proposed interventions. This will help inform planning and prioritisation to ensure the proposed actions meet community expectations.

Coral bleaching is a global issue. The resulting reef restoration technology could be shared for use in other coral reefs worldwide, helping to build Australia's international reputation for innovation.

The $6M RRAP Concept Feasibility Study identified and prioritised research and development to begin from 2019. The Australian Government allocated a further $100M for reef restoration and adaptation science as part of the $443.3M Reef Trust Partnership, through the Great Barrier Reef Foundation, announced in the 2018 Budget. This funding, over five years, will build on the work of the concept feasibility study. RRAP is being progressed by a partnership that includes the Australian Institute of Marine Science, CSIRO, the Great Barrier Reef Foundation, James Cook University, The University of Queensland, Queensland University of Technology, the Great Barrier Reef Marine Park Authority as well as researchers and experts from other organisations.

2. EXECUTIVE SUMMARY

At the core of the Reef Restoration and Adaptation Program (RRAP) are the potential actions that can be taken on the Reef – the interventions to facilitate the repair of coral reefs, to protect reefs from further damage from the effects of climate change and to promote adaptation to changing environmental conditions. These interventions have three components: the functional objective, the delivery method and the scale at which they can be applied. Functional objective types share intended benefits and have similar social and regulatory considerations. In most cases, the functional objective types contain multiple delivery methods. The first phase of the RRAP program examined the feasibility and benefits of a series of these, which are systematically described at the level of the delivery method in this report. The existing scientific evidence for the interventions and their potential benefits and risks were documented, and knowledge gaps highlighted.

The interventions evaluated can be broadly divided into two groups:

- Prevention: Interventions that focus on preventing stress from occurring.
- Treatment: Interventions that focus on repairing reefs to facilitate recovery.

To date, almost all existing interventions on coral reefs have been treatment focused, however approaches are emerging that focus on preventing or limiting stress on the Reef.

Two main categories of interventions aim to limit or prevent the amount of stress experienced by the coral holobiont during (mainly) heat waves:

1. Environmental adjustments (i.e. shading and cooling)
2. Enhanced corals using genetic tools (i.e. through breeding with naturally tolerant corals, manipulation of the symbionts or microbes, and through genetic engineering/synthetic biology).

The knowledge around many of the delivery methods for these interventions is limited and often restricted to small scale, controlled laboratory conditions. In many instances the development of methodologies is at a very early stage and will require considerable research and development prior to potential deployment on the Reef. For this reason, most prevention-focused approaches fall under "intermediate" or "high-risk" classifications in the Great Barrier Reef Marine Park Authority's permitting guidelines. Significant effort will be needed to overcome social licence issues with some of the novel and emerging technologies submitted for consideration by RRAP.

Interventions that aim to repair damage caused by disturbances on the reef to facilitate recovery fall into two main categories:

1. Active restoration (e.g. transplantation/fragmentation-type methods and enhanced larval supply through sexual reproduction).
2. Biological support to accelerate natural recovery (e.g. substrate structure and stabilisation, coral health improvement through field trials, and biocontrols).

An advantage of repair-focused intervention types (and the delivery methods they contain) is that most are already well developed and tested (albeit not necessarily on the Great Barrier Reef), and generally rely on relatively simple technologies. However, many also have limited potential to be scaled-up beyond an individual reef and thus, a key knowledge gap is how to achieve results at larger spatial scales. Based on decades of prior research and development of repair interventions and the generally small spational scales at which they have been applied, most of these interventions fall under "low" or "intermediate" risk under the Great Barrier Reef Marine Park Authority's permitting guidelines.

This report summarises the scientific knowledge of the main interventions considered during the RRAP Concept Feasibility Study and highlights current knowledge gaps in both potential efficacy and risks. This document will serve as the basis for further research and development, the modelling of potential and risks, and for prioritising interventions for the Reef going forward.

3. INTRODUCTION, BACKGROUND AND OBJECTIVES

3.1 Reef Restoration and Adaptation Program and objectives

The Reef Restoration and Adaptation Program (RRAP) aims to identify and develop a set of tools and technologies that can be used to intervene at scale on the Great Barrier Reef, and other Australian reefs, to help them recover from, and adapt to, the effects of climate change. The first phase of the program examined the benefits and risks of novel active management actions across social, economic and ecological dimensions by integrating several biophysical and ecological models and a cost/benefit and decision analysis. At the heart of these analyses were a set of **interventions** - actions that could be taken on the Great Barrier Reef (hereafter "The Reef") to achieve the stated benefit. The interventions group into **functional objective types** that share intended benefits and have similar social and regulatory considerations. Many interventions can be delivered in a number of ways – here termed **'delivery methods'**. The intervention types and delivery methods identified will require significant research and development both in terms of the product/process to be used, and the production and delivery method to apply them to the Reef. These processes, production and delivery methods identified during the concept feasibility study are described in this report (please see RRAP Report **R2—Intervention Summary** for terminology). The existing scientific literature was evaluated with respect to potential benefits and risks, noting that many of the suggested interventions are novel and poorly described in existing literature, if at all. We highlight the knowledge gaps that need to be addressed for each intervention before an informed decision can be made on its suitability for implementation on the Reef.

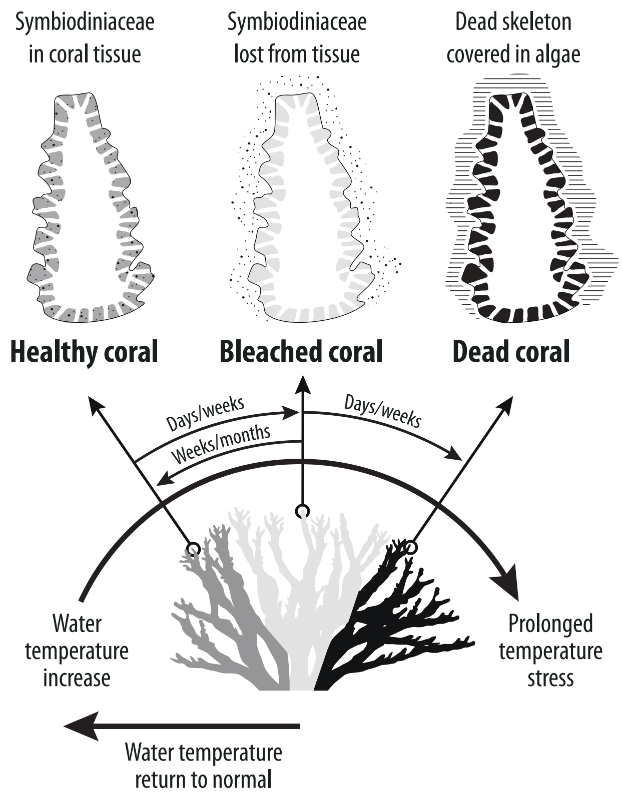
The objectives of this report are:

- To outline a spectrum of potential interventions which have been identified, and could, potentially, provide a benefit to the Reef under climate change.
- To outline current gaps in our understanding of the benefits, risks and feasibility of each intervention and delivery method.

Climate change has resulted in unprecedented declines in coral cover in recent decades (De'ath *et al.,* 2012; Hughes *et al.,* 2018), and is expected to continue causing significant disturbance and mortality events into the future. Among the most severe effects of climate change on corals reef are warming and acidification of the oceans, an increase in the frequency and intensity of tropical storms, and rapidly rising sea levels. Recent coral bleaching from ocean warming (**Box 1**) has led to wide-spread mortality around the global oceans (Hughes *et al.,* 2018). Prior to these bleaching events, tropical cyclones and crown-of-thrones starfish were arguably conidered the greatest threats to reef health (De'ath *et al.,* 2012). However, in only two years of back-to-back thermal stress (2016-2017), the Reef lost ~30 percent of its coral cover in severe bleaching events (Hughes *et al.,* 2018). The scale of devastation due to bleaching is unprecedented; therefore, ocean warming is now considered to be the most significant threat currently facing the Reef and has been re-prioritised as the focus of the interventions and delivery methods presented here. Existing technologies being trialled or implemented in other parts of the world for reef restoration are reviewed in the companion report, **T4—Current Practices**. Here we concentrate on interventions and delivery methods with the potential to make a significant impact on the Reef considering the unique challenges and opportunities of this task.

Box 1: What is coral bleaching?

Bleaching is the breakdown of the relationship between the coral host and its endosymbiotic microalgae of the family Symbiodiniaceae (Yonge and Nicholls, 1931; Coles and Brown, 2003). Coral bleaching is the primary stress response of the coral animal host to a variety of stressors including heat and occurs as a result of protein damage and oxidative stress (Davy et al. 2012). The photosynthetic pigments and/or algal cells are lost and the white skeleton becomes visible through the host tissue and corals appear bleached (Weis, 2008). High light intensity, combined with calm doldrum summer conditions, exacerbate the effect of heat stress and can increase the severity of coral bleaching (Hoegh-Guldberg, 1999). While a bleached coral can recover from an acute event through re-growth of remnant symbiont cells or the uptake of new symbionts (although limited), prolonged and/or severe heat events often lead to coral mortality (Hoegh-Guldberg 1999, Hughes et al. 2018a). In order to reduce the impacts of bleaching and mortality of corals in a warming ocean, the reduction of the effects of sea surface temperatures and/or high light is necessary. The interaction of these two physical factors may be significantly more detrimental compared with each alone.



3.2 Intervention objectives and delivery methods

RRAP aims to identify a core set of interventions analogous to ‘prevention’ and ‘treatment’ concepts in medicine and conservation. Ideally, modern medicine addresses public health problems using a combination of prevention and treatment. For example, health professionals focus on treatment of the effects of heart disease (e.g. by administering drugs and performing surgical procedures), combined with initiatives focused on prevention (i.e. improving diet and increasing exercise to prevent heart disease). Terrestrial conservation tends to take a similar approach with prevention activities (e.g. controlled burns) and treatment (e.g. re-vegetation of degraded sites). Similarly, interventions on coral reefs can focus on preventing stresses from occurring or facilitate recovery of damaged reefs. To date, the vast majority of existing interventions on coral reefs have been treatment-focused (T4—Current Practices), however novel interventions are emerging that focus on limiting stressors on reefs to prevent damage. Ultimately the aim is to provide coral reef managers with tools comparable to those available in terrestrial ecosystems, including a mix of intervention types for prevention and treatment.

The key criteria used by RRAP to evaluate potential interventions were:

1. Protect and restore key ecological functions, economic and social values of the Reef.
2. Logistically feasible to deploy at a meaningful scale.
3. Economically feasible/affordable to deploy across entire reefscapes.

It is unlikely that a single delivery method or intervention type will emerge as the ‘silver bullet’ of reef interventions and it is clear that strong action on climate change is a fundamental pre-requisite for the success of most if not all interventions. Rather, it is likely that multiple interventions will be deployed in conjunction, and as they become available. It is anticipated that a collection of effective, safe, and affordable interventions can form a holistic toolkit of measures to increase the resilience and recovery of coral on the Great Barrier Reef (Figure 1, – see also RRAP Reports R2—Intervention Summary, T6—Modelling Methods and Findings). This report summarises all of the delivery methods examined by RRAP for potential for use on the Reef.

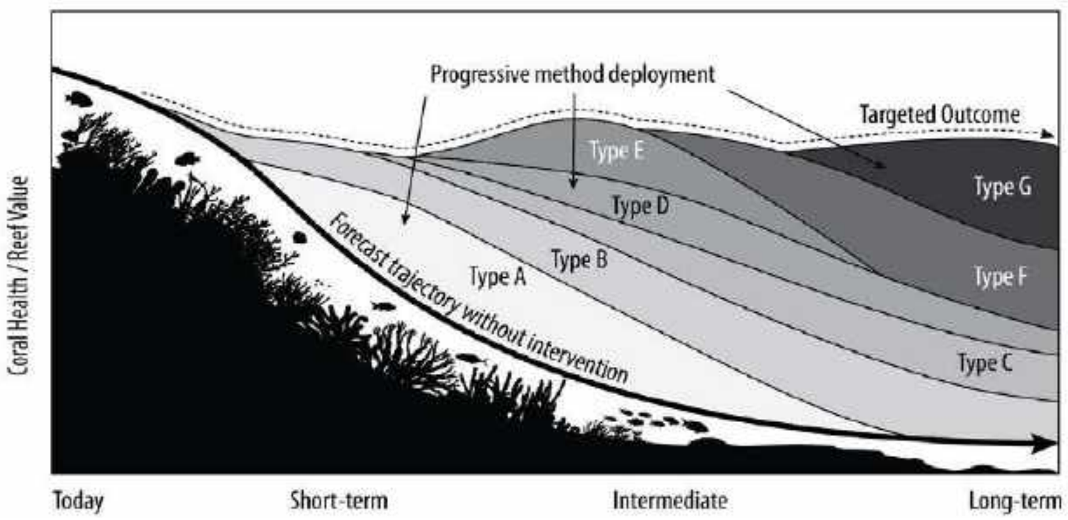


Figure 1: Conceptual diagram of the layered implementation of multiple intervention types, projected as outcomes of the RRAP. Note that this is a visual representation only, and timeframes and intervention types do not necessarily reflect actual interventions.

To achieve outcomes at the scale of the Great Barrier Reef, a combination of both prevention and repair interventions, as well as both regional and reef-scale deployment strategies offer the greatest chance of success. For example, out-planting 100 million warm-adapted corals per year on the most well-connected reefs on the Great Barrier Reef may be insufficient to meet the criteria of success unless combined with regional-scale shading or cooling strategies or effective control of crown-of-thorns starfish (**T6—Modelling Methods and Findings**). Importantly, in combination, these interventions are predicted to produce a synergistic effect with greater positive impact than the sum of the individual interventions. The challenge for RRAP is to identify how the positive impact of new interventions can be maximised: when and where, and at minimum risk and cost.

3.2.1 Prevention

Intervention types and delivery methods that fall under the **prevention** category include technologies and processes to reduce exposure to and impacts of climate change on coral reefs. For the purposes of RRAP, prevention interventions focus on ocean warming. The interventions considered here are broadly divided into two categories:

- **Regional to Reef-scale environmental adjustments** to reduce the exposure of coral reefs to events that cause acute thermal-stress, such as high temperature and ultra-violet light events. Changes to the local or regional environment may include the application of engineering processes and other technologies to cool water or shade corals at a variety of spatial scales. Examples include water column destratification, changing ocean currents, pumping cooler deep water up onto shallow reefs, reflecting heat and light from the ocean surface/water column, or reflecting heat and light through the modification of low-lying marine clouds, or atmospheric **albedo**.

- **Enhanced performance of corals** to increase the resistance of corals to conditions that induce bleaching through an enhancement of key fitness-related traits in the coral host, or those of their **microbiome**. As there are hundreds of species of coral on the Great Barrier Reef, these interventions will likely focus on a subset of species. A key area of study will be to examine if natural processes of adaptation of the coral and/or the algal and microbial symbionts can be promoted (also known as assisted evolution). This may involve the translocation of existing corals along the temperature gradient of the Reef, or the selective breeding of resilient or surviving corals from harsher environments, or disturbance event (e.g. mass bleaching). Other methods in this category use genetic engineering and synthetic biology approaches to engineer corals with enhanced performance.

Interventions that seed either local or enhanced corals onto the reef will require parallel research and development in the areas of production and delivery, ranging from the capture and transport of natural slicks to coral aquaculture and nursery know-how, to genomic and cryopreservation tools. Environmental adjustment-type approaches will require engineering innovations, especially around logistics, technology, and infrastructure, improved modelling of ocean-atmospheric processes, and improved understanding of follow-on effects. All interventions will require a full and comprehensive investigation, assessment, and mitigation of potential unintended impacts. Interventions considered in RRAP will need to be tested for social, regulatory, ethical, and Traditional Owner acceptance and approval.

3.2.2 Repair

Intervention types and delivery methods which fall under the repair category include those that aim to enhance recovery after disturbances. These interventions can be broadly divided into two groups:

- **Active restoration:** Cost-effective propagation and production and deployment of larvae, juvenile or adult stock of key species that, if restored, will provide an acceptable level of ecological function, even though biodiversity may be lower than pre-impact. Larvae, juvenile and adult corals can be produced and deployed via many delivery methods including enhanced larval supply and recruitment by deployment of laboratory-reared or wild-caught larvae or juveniles. These intervention types would typically not attempt to enhance the performance of corals but could be combined with these other approaches through a deliberate selection of donor stock.

- **Biological support to accelerate natural recovery:** Creating artificial reef structures, or modifying reef substrate, to enhance natural coral recruitment. This involves the stabilisation of rubble and/or the deployment of optimised, artificial structures and surfaces to enhance coral recruitment, growth and survival of juveniles derived from natural, field or laboratory conditions. Other approaches focus on facilitating rapid recovery of bleached corals. This could occur through direct treatment of disease, nutrient supplementation through probiotics, feeding or other methods.

3.2.3 Species diversity and ecological interactions

A fundamental goal of ecological restoration is to restore ecosystem functioning, which requires a complete suite of species assemblages, preferably indistinguishable from pristine, pre-disturbance communities (Society for Ecological Restoration International Science & Policy Working Group 2004). Indeed, the health of an ecosystem can generally be estimated from the diversity of species within the system. However, it is often not feasible to focus interventions on every single species in an ecosystem and instead, many intervention methods are forced to focus on a subset of ecologically significant target species, such as foundational or keystone species, or structural ecosystem builders. Further, interventions may have unintended effects when implemented, which could transform reefs into novel ecosystems. This forces difficult trade-offs that require weighing ecosystem function against historical ecosystem composition (Anthony *et al.,* 2017). However, the risk of creating an ecosystem with lower diversity than pre-impact needs to be viewed in the context of potentially losing the system in its entirety, if no interventions are implemented.

The Great Barrier Reef hosts a diverse range of coral species (more than 600), however more than 75 percent of the overall coral cover is provided by species from nine genera (*Acropora*, *Pocillopora*, *Porites*, *Montipora*, *Diploastrea*, *Stylophora*, *Goniastrea*, *Echinopora* and *Favia*; Figure 2). While the whole suite of corals species present on the Great Barrier Reef contributes to the functioning of the ecosystem, restoration projects might most effectively support the resilience of the Reef by focusing on species from these nine dominant genera. Further, while a diversity of species is important to ecosystem function, diversity of growth morphologies is also critical to maximise the variety of habitats for other non-coral Reef biota. In RRAP, it is envisaged species selection will be guided by our knowledge of the system (i.e. with data from the Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program) to recover the function of an ecosystem that is largely built by nine genera.

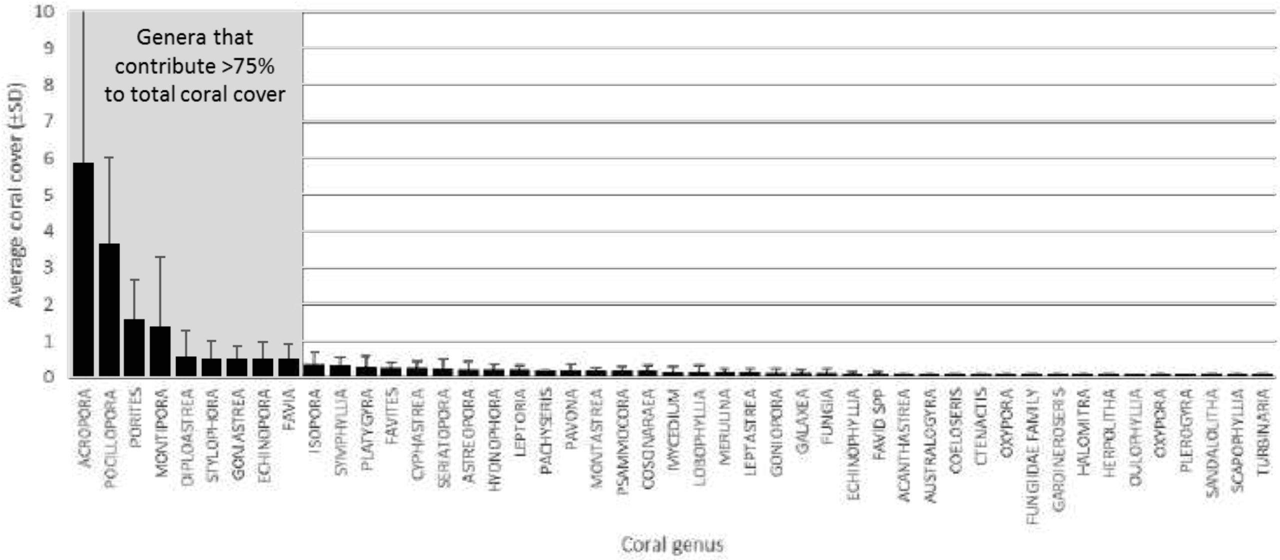


Figure 2: Average coral cover across mid-shelf and offshore reefs of the central Great Barrier Reef from the Cairns and Townsville sectors from 2017-2018 by coral genus (source: AIMS Long-Term Monitoring Program). All genera that contribute more than 0.5 percent coral cover are included. Shaded area represents those genera that contribute > 75 percent coral cover combined.

4. TYPES OF 'PREVENTION' INTERVENTIONS

4.1 Environmental adjustments that cool or shade reef waters

4.1.1 Shading

Mass coral bleaching is caused by warmer than normal water temperatures. Although it can be induced in the dark (Tolleter *et al.*, 2013; Bessell-Browne *et al.*, 2017), it is generally exacerbated by light (Coles and Jokiel, 1978; Gleason and Wellington, 1993; Lesser and Farrell, 2004). Any natural or human-enhanced conditions that decrease solar irradiance, such as cloud cover, natural shade or high turbidity, can offer protection to corals under thermal stress (Hoegh-Guldberg, 1999; Goreau *et al.*, 2000; Mumby *et al.*, 2001; West and Salm, 2003; Wagner *et al.*, 2008; Golbuu *et al.*, 2011). It is therefore feasible to reduce or avoid bleaching during marine heatwaves if light levels could be attenuated through **shading**. Direct evidence for this hypothesis mostly comes from aquarium conditions (Lesser and Farrell 2004; Smith and Birkeland 2007; Coelho *et al.*, 2017) but is also evident from observations of mass bleaching in the field (Leahy *et al.*, 2013; Hoogenboom *et al.*, 2017; Hughes *et al.*, 2017). Therefore, shading poses a direct adjustment of the environment that could be strategically deployed in summer months, or in response to bleaching forecasts (Coelho et al., 2017). While all shading interventions considered by RRAP are aimed at blocking incoming light, some are likely to be limited to individual reef-scale deployment due to logistical constraints. Others could be scaled-up to larger regional application, targeting both a reduction in light and cooling of ocean surface waters.

While shading and cooling may reduce the stress experienced by corals during a heat event, there is a possibility of diminishing corals' adaptation and/or acclimatisation to extreme conditions. A potential risk with shading is therefore to inadvertently slow **'hard' natural selection** through mortality events for more tolerant coral species or symbionts (Donner *et al.,* 2005, Hughes *et al.,* 2018a), potentially forcing shading to become a permanent requirement on reefs under future-predicted climate scenarios where emissions are not reduced quickly enough to stabilise temperatures. However, there is growing evidence that corals are capable of adapting to increasing temperatures through **'soft' natural selection** (Matz *et al.,* 2018), which would occur outside times where intermittent shading would be applied. The same consideration applies to environmental adjustments which cool water temperatures. Environmental adjustment interventions such as shading appear to have a reasonable level of control in terms of how much is applied. Understanding then, the interplay between environmental stress, its manipulation, and rates of adaptation will be critical to managing any environmental adjustment-type interventions for long-term benefit.

Other potential undesirable impacts common to all shading techniques include over-shading of light-limited corals or other autotrophic biota such as seagrass, as well as reduced coral growth rates and reduced rate of translocation of photosynthates from symbionts to corals. Further, risks associated with the required infrastructure, such as contamination to the marine environment or the creation of habitat and stepping-stones for invasive species and pests should be considered. Some undesirable consequences, particularly those related to over-shading of light-limited organisms are less of a concern for individual reef-scale intervention, as they can be mitigated by prudent site selection and limited shading duration. On the other hand, regional scale shading options achieve the outcome by much less shading intensity over a much larger area, the total amount of shading for inteventions at this scale may not differ markedly from natural variability due to atmospheric conditions.

However regional-scale deployment carries further risks, as successful cooling of ocean waters may alter local climate and increase the capacity of the ocean to absorb CO_2, leading to higher acidity (Robock, 2011). It can also be argued that these impacts should be evaluated against the pre-industrial case rather than that of the current anthropogenically-altered climate. Critically, all forms of intervention will carry multiple types of risk and potential benefits which will need to be evaluated and weighed against the risks and potential benefits of not intervening.

Surface films

The deployment of ultra-thin surface films aims to reduce solar radiation reaching corals (ultraviolet [UV] stress on corals and photosynthetically active radiation [PAR] stress on symbiont photosystems). Under certain conditions (e.g. in very shallow water) it may also affect local water temperature (visible light and infrared radiation heating up the water), although this requires further testing to determine at what scales it could make a meaningful difference to heat-stressed corals. This potential intervention proposes to reduce stress on corals and other photosynthesising organisms during heat wave conditions (**Figure 3**). Its basis stems from efforts to reduce evaporation in open water storage units, such as reservoirs and dams, using ultra-thin surface films (Barnes, 2008). The technology is currently being researched and developed to aid in the protection of the Great Barrier Reef. Early laboratory trial findings suggest surface films can be stable, attenuate light by approximately 20 percent across the spectrum (including UV), are non-toxic to corals (made from calcium carbonate and biodegradable) and protect some coral species from bleaching (Qiao et al 2017). The application of ultra-thin films could be implemented without permanent infrastructure and would only need to be applied when bleaching conditions are predicted.

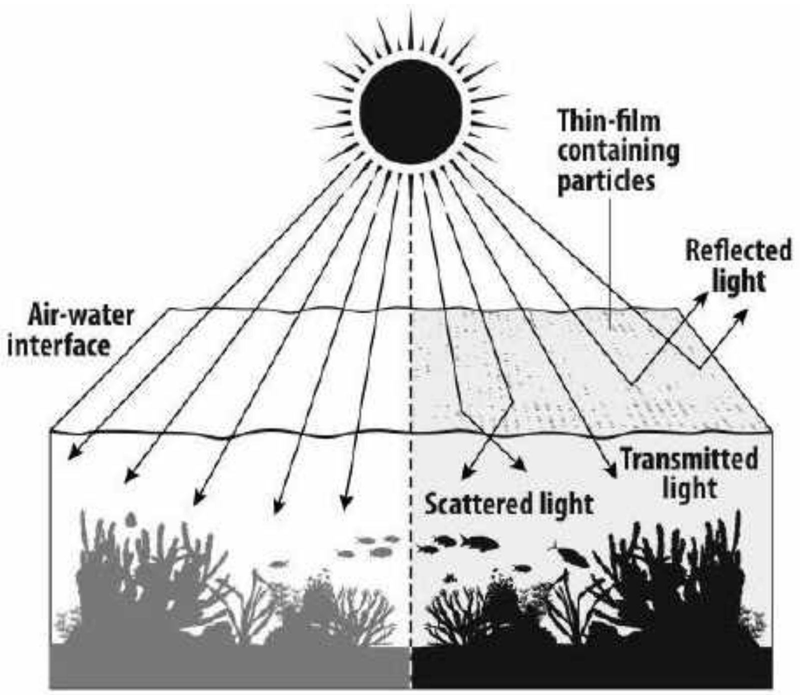


Figure 3: Surface films aims to reduce the stress corals and other photosynthesising organisms experience during heatwave conditions, by scattering and reflecting incoming sunlight. Reproduced with permission by the lead author and Great Barrier Reef Foundation.

While early phase trials are still underway, technical aspects of deployment are being considered. Potential deployment methods of surface films include air (drone or plane), vessel, or automated buoy. Deployment would be reef-specific, following bleaching forecasts and predictive oceanographic modelling. It would likely target high-value reefs with long water retention times. Mechanisms for automated deployment and regeneration of surface films during a bleaching event are being considered. This intervention should be focused on ecologically important seed reefs to improve recovery of nearby reefs. Further, surface films could be combined with coral seeding, crown-of-thorns starfish and *Drupella* management measures at high-value reefs, to benefit tourism and industry.

The maximum stability of the film in large tank studies is less than 48 hours. Realistic targets for reduction in light levels are around 20 percent in the field, mitigating the risks associated with over-shading. Further testing and development is required to improve attenuation and behaviour of surface films, test efficacy, longevity (including stability and strength) and environmental safety (and post-breakdown effects), and to model both direct irradiance and heat load benefits.

Shade cloth deployments

The primary goal of providing shade (with cloth or organic material including algae) is to reduce the levels of UV light and PAR on the coral holobiont, thereby reducing levels of bleaching and mortality in targeted corals on reefs. The suggestion that shade cloth might be used to prevent corals from bleaching has been around since at least 2006 (AAP 2006, Rau *et al.,* 2012). The shading approach has been demonstrated in aquaria (Lesser and Farrell, 2004; Smith and Birkeland, 2007) and can reduce levels of bleaching (Coelho *et al.*, 2017). In the field, subsurface shading has been shown to reduce the bleaching colour score in a reef pool (Coelho *et al.*, 2017), but the experiment did not extend to the point of inducing mortality so it is not clear how effective it might be under more severe conditions. Shade cloth deployments have been trialed at small scales on Agincourt Reef by an ecotourism group (QuickSilver's Reef Biosearch; AAP, 2006) but the results are not presently available.

Deployment of shade cloth would most likely involve suspension of shades at or near the surface by a system of floats and anchors, and, as such, create a site-specific deployment unit on the spatial scale of 100m^2. In order to scale-up this intervention, multiple shades would need to be engineered to allow low-cost and rapid deployment and retrieval without causing damage to the reef. Full retrieval is likely necessary for cleaning of fouling organisms and maintenance, as well as to avoid damage and deterioration by cyclones and storms.

This intervention would be immediately available in terms of its technical aspects. However, such applications carry risk of unintended physical damage to reef corals and structure from anchors or breakage of the shade cloth suspension system and would require appropriate high-risk permits. As with any artificial structures added to the reef, these surfaces will become substrate for microbes and other organisms. Non – natural substrates tend to have increased likelihood of supporting invasive species (Glasby *et al.,* 2007, Tyrell and Byers 2007, Ruiz *et al.,* 2009). If the shade cloths themselves are in the water, then the surface area will be very large potentially increasing this risk. The risk is offset however if shade cloths are deployed for short periods of weeks to months during thermally stressful periods and then recovered and stored until next needed. Although this intervention is short-term, knowledge gaps exist regarding indirect effects such as changes to water temperature, photosynthesis, and primary production (i.e. changes to algal assemblages). These risks would increase if the application was to be scaled up.

Ocean microbubbles

Microbubbles of air suspended in the surface ocean reflect incoming sunlight in a very similar way to droplets of water suspended in air (i.e. clouds or fog), albeit with less efficiency, due to the absorption of backscattered light in ocean waters (Seitz 2011). Generation of large quantities of microbubbles in the surface ocean has been suggested for use in global-scale geoengineering (Forster et al. 2014; Seitz 2011), but could also be applied at a local or regional scale (Seitz 2011). Microbubbles can be generated in the upper few metres of the ocean and are expected to persist from hours to days. Both the lifetime and reflectance of the microbubbles are expected to increase with the concentration of surfactants in the seawater. Microbubbles coated with organic film increase the reflectance as much as 400 percent based on modelling and observations of natural microbubbles (Zhang et al. 1998). This may occur naturally in the Great Barrier Reef due to coral-secreted surface-active compounds (Deacon 1979), or potentially through the co-application of biologically-benign organic surfactants with the generation of microbubbles (Seitz 2011).

Microbubbles can be generated through several means, such as by methods involving expansion of air-saturated water through vortex nozzles, ultrasonic excitation, and fluidic oscillation—the last of which may be the most energy efficient (William *et al.* 2008). Crook et al (2016) suggests adding surfactants to the wake of ships could prolong the lifetime of microbubbles in the ships' wake (Figure 4), a technique which could be employed on the Reef as part of a regional solar radiation management strategy.

Figure 4: The albedo effect of bubbles in the surface ocean is visually apparent from ship wake. Microbubbles would persist for days in comparison to the much larger ship wake bubbles which only persist for minutes to hours. Image credit: Chris Cardinal.

It is conceivable microbubbles could be applied at either an individual reef scale, for shading, or operated more continuously at a regional scale for both shading and cooling, as an alternative or supplement to atmospheric interventions described below.

Given microbubbles are dispersed by ocean currents rather than winds, they are expected to spread more slowly than interventions released into the air. Therefore, if regional cooling is targeted using microbubbles, it would require comparatively more 'stations' than would be required with atmospheric shading interventions. However, if microbubbles were found to be safe for shallow coral reef habitats, their slower dispersion may prove an advantage for targeting shading to an individual reef, leading to longer residence times and increased efficacy.

Risks specific to the microbubble approach for global-scale geoengineering have been pointed out by Robock (2011) but remain as yet undocumented. Of these, most relevant to local-scale application are the potential for adverse impacts if surfactants are added to promote bubble lifetime, the unknown impact of the bubbles themselves on marine biota, including corals, and regional climate impacts from the cooling of surface waters. The production of microbubbles would require surface-based infrastructure, either stationary or vessel-based, leading to associated risks of equipment malfunction or destruction, creating marine debris.

Marine cloud brightening

Marine cloud brightening (**Figure 5**) has been suggested as a method of mitigating bleaching on the Reef by increasing the reflectivity (known as albedo) of low-altitude marine clouds over the Reef, to reflect the sun's incoming solar radiation back into space (Harrison, 2018). This intervention would both cool and shade surface waters over regional-scale areas. The combined effects of decreased sea surface temperatures and lower light levels are expected to reduce coral bleaching. Local cloud brightening from cargo-ship exhausts has long been identified in satellite imagery in regions of the world where large, persistent decks of marine stratocumulus coulds commonly occur, providing in some cases an unambiguous, visually-detectable example of albedo increase (e.g. **Figure 5**).

Regional cloud modification (for the purpose of enhancing rain or snowfall) is extensively and regularly practiced around the globe. In Australia, both Snowy Mountains Hydro and Tasmania Hydro use the technique to produce hydroelectricity. Legislation in Australia specifically permits cloud seeding activities in the Snowy Mountains alpine national park (Snowy Mountains Cloud Seeding Act 2014) which may provide a basis for legislation regulating marine cloud brightening for coral bleaching mitigation in the future.

Cloud brightening would provide shading and cooling through two mechanisms:

1. A direct effect from sprayed seawater droplets (which does not require clouds to be present)
2. Through indirect effects of the sea salt particles brightening low lying clouds, from which the technology derives its name.

Figure 5: Cloud brightening due to marine ship exhaust is a visually detectable occurrence due to the high albedo change which occurs under certain atmospheric conditions. These conditions are not often present on the Reef, but modelling (see Report T14- Environmental Modelling of Solar Radiation Management) has indicated that low-level clouds on the Reef are amenable to a lower intensity of brightening. Image credit: NASA.

The technology is sometimes referred to as marine sky brightening (e.g. Stjern *et al.,* 2018), particularly when targeted at regions or periods without suitable cloud formations. While the atmosphere of the Great Barrier Reef is not characterised by the persistent decks of marine stratocumulus cloud considered ideal for cloud brightening, there is a reasonable fraction of low cloud during summer bleaching conditions, which preliminary atmospheric modelling has indicated to be susceptible to cloud brightening (see **T14—Environmental Modelling of Large Scale Solar Radiation Management**).Studies examining the global sensitivity to marine cloud brightening have also shown the Reef region to be suitable and amongst the most responsive (Alterskjær *et al.,* 2012).

The process works by supplying additional sea salt aerosols to regions where droplet density is limited within low-lying marine stratocumulus clouds (Latham, 1990). Aerosols can be provided in the form of nano-sized salt crystals produced by spraying sub-micron-sized seawater droplets into the atmospheric boundary layer and allowing them to evaporate (Latham *et al.,* 2012a). Alternatively, vaporised oil through deliberate heating of oil, or through the combustion of crude oil in cargo ships, has long been known to increase the albedo of clouds (Russell et al 2013). The portion of nano-sized aerosols that reach the cloud condensation level act as additional cloud condensation nuclei. Additional cloud condensation nuclei affect the droplet size distribution within clouds by increasing the number of droplets while decreasing the mean droplet size. This results in a cloud with higher albedo, that reflects a greater portion of incoming solar radiation back into space (Twomey, 1991). When salt is used, this cloud albedo effect is enhanced by the albedo of salt crystals themselves, regardless of whether cloud is present or not (Ahlm *et al.,* 2017), and also because ‘brightened’ cloud is less likely to precipitate and thus may remain in state longer (Albrecht, 1989). Marine cloud brightening aims to replicate natural processes of sea salt aerosol generation by the ocean, and also mimic, less exactly, the generation of sulfur-based aerosols by corals and algae (through the production of dimethyl sulfide; DMS), which is also hypothesised to be linked to low-level cloud albedo on the Reef (Jones *et al.,* 2017).

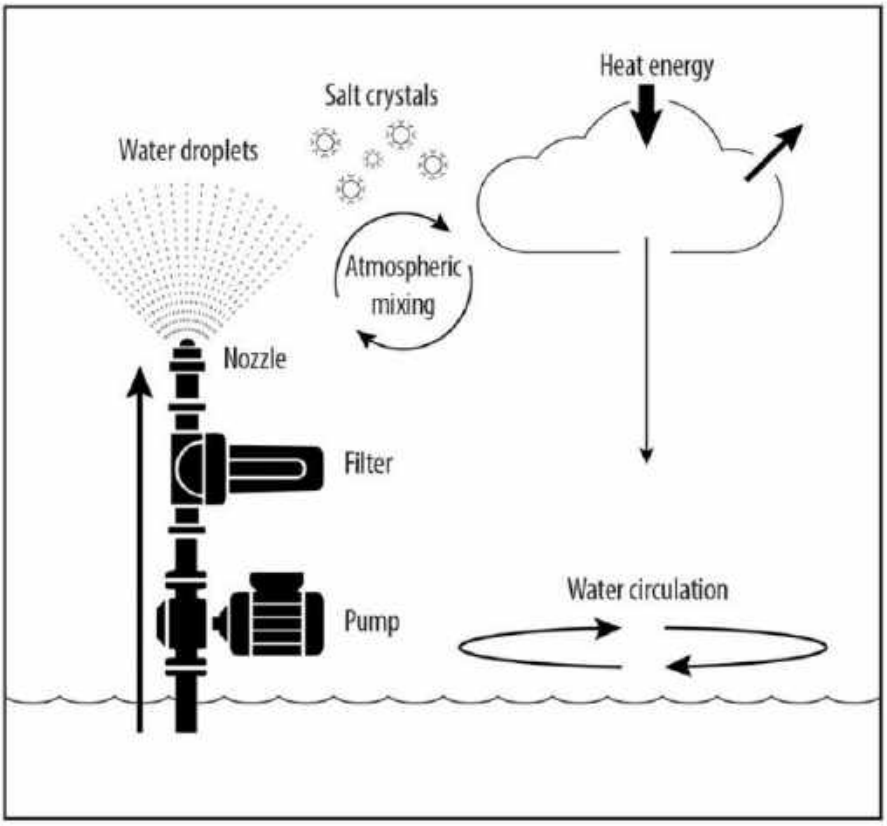


Figure 6: Marine cloud brightening aims to increase the portion of incoming solar radiation reflected back into space (i.e. albedo). Figure used with permission from Harrison (2018).

The benefits of cloud brightening are cumulative over time. eReefs hydrodynamic modelling shows that approximately two weeks of operation is required to reach full cooling effect, although this is expected to depend on the size of the region over which marine cloud brightening is operated (Harrison, 2018). Marine cloud brightening technology has the potential to significantly relieve bleaching stress over large portions of the Reef (i.e. regional spatial scale), simultaneously reduce mixed-layer temperatures, and provide shade over these areas. To be effective on the Great Barrier Reef, marine cloud brightening would need to operate continuously over weeks to months, when satellite-based warning systems indicate the risk of bleaching to be high. The input materials are seawater and energy. The energy could potentially be supplied by renewable sources (e.g. solar, wave, current, or wind). Cloud brightening stations would be analogous to snow-making cannons, including a fan, for initial dispersion of the droplets and around 400 atomising nozzles to produce ~1.2 quadrillion (10^{15}) nano-sized aerosols per secondfrom 1.6 L/s of seawater (Figure 6) (Cooper *et al.*, 2014).

Potential undesired impacts include the possibility of changing local weather and rainfall patterns, an issue comparable to that of cloud seeding. Recent studies hypothesise a link between rainfall in north-east Queensland on aerosols currently produced by Reef corals (Jones & Ristovski, 2010). At this time, it is unclear whether cloud brightening over the Reef would increase, decrease, or have negligible impact on rainfall over the impacted regions. Cooling of sea surface temperatures may well have a larger impact on weather patterns than the aerosol interactions with cloud. Similar risks to other shading techniques must also be considered (such as reduced productivity), however these may be of lower impact as the marine cloud brightening principle works though a lower reduction in shortwave solar radiation, spread over a longer period (weeks to months).

Nearly 30 years' of research into application of marine cloud brightening on a global basis to cool the planet and offset anthropogenic warming have refined the theory (Latham *et al.*, 2012b), but progression to field experiments and trials has been slowed by controversy surrounding proposals to deliberately alter the global climate, so called 'geoengineering' (Wood and Ackerman, 2013). Geoengineering acts on a global scale, by attempting to alter climate mainly through greenhouse gas removal, or global-scale solar radiation management. In contrast, marine cloud brightening, applied either regionally or over the entire Great Barrier Reef during marine heatwaves, presents a significantly different risk profile, which is yet to be comprehensively evaluated. In addition to social, ethical, and environmental considerations, there remains considerable feasibility, engineering, and experimental work to develop marine cloud brightening technology to readiness for trials.

Misting

Misting refers to an intervention where particles are distributed into the atmosphere over the Reef by vaporising a biogenic oil to form a mist of reflective smoke particles, to reduce incoming solar radiation. This is the same technology used in 'smoke' machines for recreational activities such as concerts, the sport of paintball, and in the special effects industry. The solar forcing is analogous to the cloud brightening direct effect (i.e. reflection due to the seawater droplets themselves in the absence of cloud) and can be considered an alternative method of marine sky brightening. The primary differences are that seawater is not used to produce the atmospheric particles, and that the aerosol direct effect is targeted, rather than the aerosol indirect interactions with clouds. Nevertheless, aerosol indirect effects on cloud formation and microphysics will still inadvertently occur, such that at large enough scales, the impacts of misting on clouds may be very similar to that of cloud brightening. For example, misting generators have been used previously in field experiments to examine the cloud microphysical and albedo impacts of additional aerosols (e.g. Russell *et al.,* 2013).

Generators to produce white smoke from vaporising oil are available for a variety of applications, from the movie special effects industry to military applications where they are operated by defence forces around the world to obscure the field of battle. A commonly employed method is to use the hot exhaust gases of a pulsejet turbine engine to vaporise oil. The military grade of technology is the most suitable for producing large quantities of solar obscurant.

Misting could conceivably be operated on a local scale, such as that of an individual reef or collection of reefs. Operated in this manner, the primary effect would be shading to reduce the light component of stress on corals. There may also be some transient localised cooling of shallow waters within individual reef lagoons due to the shading — as with surface films. Alternatively, it may be possible to operate misting on a regional scale, similar to cloud brightening, by employing a large number of generators distributed throughout the region and relying on atmospheric mixing and advection to distribute the generated particles. In this scenario, the radiative forcing effect would be similar to that of cloud brightening, acting to both lower sea surface temperatures and reduce light stress on corals.

The risks of misting on a regional scale are comparable to those of cloud brightening. At an individual reef scale, the risk of over-shading is potentially high, as the shading will be more intense in regions immediately around the generator. This impact could be reduced if the generator was mounted on a moving vessel. Misting carries some additional undesirable impacts such as decreased visual amenity and potential safety considerations to vehicles (aircraft/ships) and human health in the immediate vicinity of the generators. It is likely that some area of exclusion to other marine park users would be required in the vicinity of operating generators. Development of this technique is dependent upon selecting a suitable biogenic oil, perhaps derived from phytoplankton, which would not pose an unacceptable risk to the Reef marine environment. Commonly used military fog oil, a severely refined white mineral oil (NAS 1997), is not anticipated to be suitable for use on the Great Barrier Reef.

Figure 7: Mist over the ocean.

Fogging

Producing a low hanging 'sea fog' of seawater droplets is a potential solar radiation management technique. Producing sea water droplets an order of magnitude (or so) larger than for marine cloud brightening would be roughly equivalent to the properties of a heavy sea fog (Figure 8). Although the process of pumping seawater and spraying it into the marine boundary layer is almost identical to that of marine cloud brightening, the target effects, lifecycle of the produced droplets, and probable scale are quite different.

Droplets of order 10μm would tend to hang low in the marine boundary layer, unlike nano-sized droplets produced for cloud brightening. They would experience a much shorter lifetime before predominately falling back into the ocean. Equivalent to the direct effect of marine cloud brightening and misting, the droplets produced by fogging would reduce the incoming shortwave solar radiation, providing shading. Their evaporation near the sea surface would lead to evaporative cooling of the air mass in which they were suspended, potentially providing cooling by both shading and by sensible heat flux into the ocean surface waters. As with misting, fogging could conceivably be applied at the scale of individual reef or collection of reefs. Subject to energy and logistical requirements, it may also be possible to operate fogging over a larger local or regional area. Commercial fogging systems are commonly used in industrial processes to provide either cooling (by evaporation) or dust suppression.

Generating a sea fog formed of seawater particles is expected to be relatively environmentally benign. Risks include those associated with over-shading, suppression of natural adaptation, and infrastructure risks. Modelling has not yet been performed to evaluate the various components of the ocean–atmosphere heat flux. While evaporative cooling of the air above the ocean will tend to cool the ocean by adjusting the sensible heat flux, the increased humidity will tend to suppress evaporative cooling of the ocean surface (latent heat flux). The net heat flux change induced by the evaporative cooling is therefore unquantified. However, the large particle size of sea water droplets in the fog can be expected to create significant shading to the extent that the fog can be maintained over the target region.

4.1.2 Vertical mixing

Vertical mixing is an upward or downward movement of water that occurs as a result of temperature gradients in the oceans. It occurs naturally on scales from 10 - 1000km. Mixing of waters on the Great Barrier Reef is partly facilitated by wind, however this process may fail during summer doldrum conditions. If these conditions persist over several days, it may contribute to the severity of coral bleaching events (West and Salm 2003, Bainbridge 2017). The mechanics of this natural phenomenon can be engineered on smaller spatial scales to manipulate water temperatures and circulation patterns; hence, a role for vertical mixing technologies has been proposed to, and/or aid in, reef maintenance and restoration. It has been hypothesised that benefits can be achieved either by creating mixing during summer doldrum conditions, or by pumping cooler waters from depth.

The primary objective of vertical mixing technologies is to reduce temperature in shallow reef environments, thus reducing the thermal exposure of corals (measured in degree heating weeks) and subsequent bleaching and mortality. There is evidence that, in certain locations, natural upwelling of cooler water from below the thermocline can reduce the local occurrence of bleaching (e.g. Eidens *et al.*, 2012).

Currently, there are two main ways to artificially increase vertical mixing in a reef environment: by using slow-moving impellers to ‘turn over’ shallow water, or by pumping quantities of cool water from depth. Both vertical mixing technologies require substantial infrastructure. Therefore, they carry the risk of equipment failure and potential reef damage during construction or deployment, as well as potential aesthetic and noise considerations, which may affect their social acceptability. Introducing artificial structures into the marine environment also carries a risk of supporting algae, other microorganism, and invasive species. As discussed above for shade cloths, the risk may be worsened for vertical mixing infrastructure that is required to be permenantly in place. Further, similar to shading technologies, there is a possibility that these techniques may prevent natural acclimatisation to thermal extremes, by preventing natural selection during heat waves.

Underwater impellers

Vertical mixing of the water column can be achieved through submerged, slow-moving, solar-powered impellers or fans. The primary objective of these systems is to reduce the shallow water temperature stress by mimicking normal mixing processes during summer doldrum conditions, at very small scales (e.g. that of a 'snorkelling footprint' associated with a reef tourism site **Figure 9**). The proposed ecological benefits of underwater impellers include reducing or avoiding heat stress to reef species during heat wave conditions. This intervention is based on approaches to break down stratification in static water bodies such as lakes and dams (Kirke and Gezawy, 1997; Kirke, 2000) where it has been employed for more than 40 years (Kirke, 2000).

A trial research program (*Reef Havens Research Project)* is being implemented at Moore Reef in the Northern Great Barrier Reef. At the site, an in-water monitoring array has been established that allows testing of interventions aiming to mimic normal water column mixing, such as impellers. The deployment and use of impellers will be temporary (as they are only needed during doldrum summer periods), and site-specific, planned to target high-value tourism sites (350-500 m^2), with low potential to upscale beyond selected reefs.The efficacy of the underwater impeller interventions will depend on natural water circulation at the site, the residence time of water within the reef lagoon (e.g. turbulence, flow) as well as the depth of the thermocline.

Further development and modelling are required to determine the capacity of the impellers to move, mix and maintain water in unconstrained marine environments. The Reef Havens research project assessed the risk of depositing excess nutrients on the reef as low, given the mixing intervention is only aiming to mimic normal water column mixing that has suffered short-term failure due to doldrum conditions. The project will monitor flow, temperature, coral light stress, and the depth of stratification that occurs during doldrum conditions. The Great Barrier Reef Marine Park Authority classifies this intervention as a high-risk activity since it requires installation of facilities and large infrastructure that will require maintenance and may be sensitive to local weather and storms.

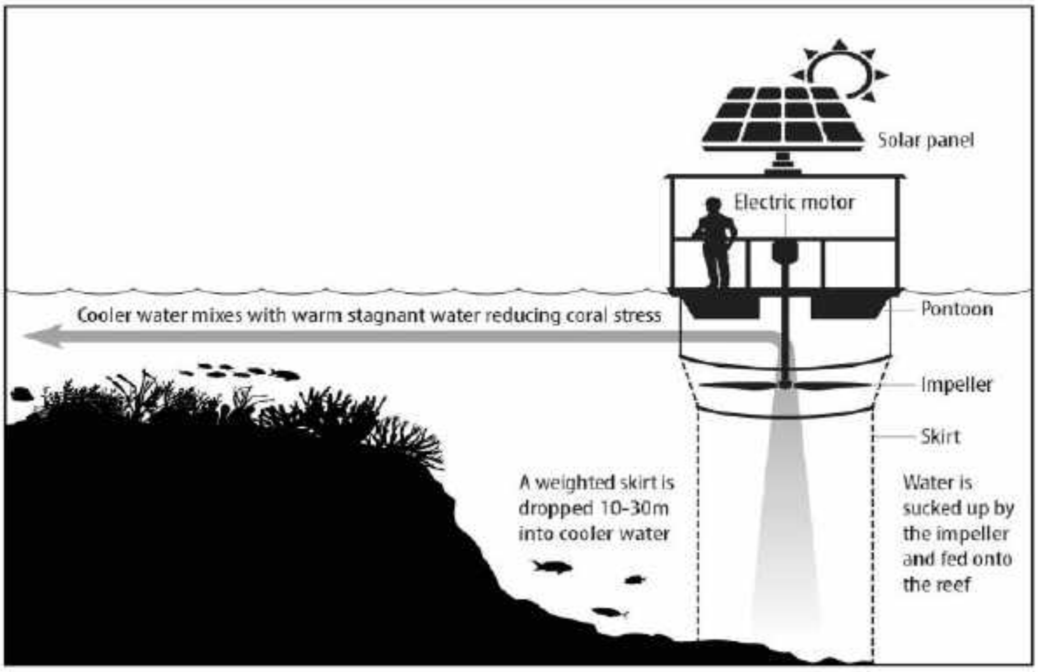


Figure 8 – A schematic of a solar-powered underwater impeller system (image modified with permission, Reef and Rainforest Research Centre).

Pumping and mixing

Cooling of surface waters can be achieved by mixing warm surface waters with cooler water from below the thermocline. The technique uses pumps to move water from a depth sufficient to achieve a temperature gradient and mix this with warm surface waters during summer doldrum conditions. Successful cooling of waters may prevent bleaching, thus preserving whole reefs, supporting overall reef biodiversity and functionality. The input of nutrient-rich, deep water may boost productivity of reef fisheries, which could provide beneficial nutrient inputs for corals or negatively impact corals through indirect effects. These impacts on corals (both negative and positive) must be effectively understood and managed prior to deployment.

The input of deep-water nutrients is one of the main ecological risks of the pumping and mixing method, especially given that substantial volumes of water would mean nutrient inputs were commensurately large (Rocheleau and Grandelli, 2011; Lapointe, 1997). This could lead to eutrophication of the water column, a destabilisation of internal nutrient dynamics of corals, potentially exacerbating thermal sensitivity (Morris et al 2019) and blooms of benthic algae. Further, nutrient enrichment from deeper waters could lead to phytoplankton blooms, enhanced survival of crown-of-thorns larvae, and changes in overall water chemistry on the reef (e.g. decreased oxygen). In addition, the equipment could contribute to noise and visual pollution.

Further research into the physiological mechanisms underpinning bleaching are required to assess whether a ‘safe’ balance of temperature reduction and nutrient limitation is possible. Potential effects could also be mitigated by operating the shallow-water cooling scheme intermittently, when required, and releasing deep water back below the thermocline at other times. The technique may be possible to combine with **Ocean Thermal Energy Conversion** (OTEC, **Box 2**) plants to generate electricity to power the pumps, although this requires further research.

Box 2: What is OTEC?

Ocean Thermal Energy Conversion (OTEC) can produce electricity by using the temperature difference between deep, cold ocean water and warm, tropical surface waters. OTEC plants simultaneously pump large quantities of cold seawater from the deep ocean and warm surface seawater through heat exchangers, to run a power cycle and produce electricity. Generally, a temperature differential of at least 20°C is required (**https://www.tudelft.nl/ocean-energy/research/thermal-gradient-otec**). Once established, such plants would provide the energy required for pumping limiting the amount of external energy which would need to be supplied. Existing plants around the world are mainly used for air conditioning and electricity generation; none are used to manage surface seawater temperature. Therefore, returning subsurface water is recirculated to depths below the thermocline, to prevent any ecological effects on the surface ocean layers.

OTEC uses warm (around 25°C) surface waters to vaporize a working fluid with a low-boiling point (e.g. ammonia). The vapour expands and spins a turbine coupled to a generator to produce electricity. The vapour is then cooled by seawater pumped from cooler depths (5°C) and condenses back into a liquid, ready to be reused in a continuous electricity-generating cycle. OTEC systems require very large volumes of water (over 44,000m^3 per minute for a 100MW generator), which have the potential for cooling substantial areas of reef. However, an extensive diffuser network would be required, along with sophisticated modelling and control systems, in order to create even levels of cooling.

4.2 Enhanced performance of corals

Enhanced stress tolerance (or other desirable trait) of the coral holobiont via accelerated evolution

Corals can be described as **holobionts**, a collective of the coral animal and communities of eukaryotic and prokaryotic microorganisms (Rohwer *et al.*, 2002; Ainsworth *et al.*, 2010). The health, physiology, and stress tolerance of the coral holobiont is attributed to the symbioses between the coral animal, photosynthetic endosymbionts (many species from the family Symbiodiniaceae), and beneficial bacteria, viruses and fungi. Demographic attributes of coral host populations, such as long generation times (~4 - 40 years: Babcock, 1991; van Oppen *et al.,* 2011b), have formed the basis of arguments that coral host adaptation cannot keep pace with the increasing rates of global warming (Hoegh-Guldberg, 2014). Emerging evidence from genetically diverse populations across multiple invertebrate taxa show that a redistribution of existing genetic variation can support relatively rapid adaptive response (Messer & Petrov, 2013; Whiteley *et al.*, 2015; Torda *et al.*, 2017). Additionally, the coral-associated **microbial** communities (i.e. Symbiodiniaceae species, bacteria, viruses, fungi) may provide significant contributions to the adaptive potential of the coral holobiont due to their orders of magnitude greater diversity, shorter generation times (e.g. Wilkerson *et al.*, 1988) and overall high **functional diversity** (Stat *et al.*, 2008; Torda *et al.*, 2017; van Oppen et al 2015). These mechanisms support the possibility of accelerated adaptation to climate change conditions through **assisted evolution**.

The functional objective of the following interventions is to increase the resilience of corals by enhancing their stress tolerance to acute and chronic ocean warming (van Oppen *et al.*, 2017). This can target one or more of the holobiont partners (Jones and Monaco, 2009; van Oppen *et al.*, 2015; **Figure 10**). Specifically, the interventions summarised here may target the host potential for acclimatisation and adaptation (five delivery methods) or alternatively, the potential of the microbial partners (three delivery methods) (Figure 10). These approaches could, in principle, be applied to any trait of importance including tolerance to other stressors (e.g. disease), calcification and growth rates or other important traits for survival. Traits can be correlated, which can increase or decrease rates of adaptive evolution, depending on whether they are negatively or positively associated with each other (Sunday *et al.*, 2014). Therefore, it is critical to adopt a holistic approach in the development and application of corals with enhanced performance, in order to avoid accidental adverse trade offs and the degradation of genetic diversity. The mechanisms by which a focal trait (e.g. thermal stress tolerance) can be enhanced include:

- **Physiological acclimatisation** where a shift in the organism's phenotype is achieved through physiological adjustments, potentially under heritable or epigenetic control (Coles and Brown 2003; Weis 2010; Brown and Cossins 2011; Sanford and Kelly 2011).

- **Genetic adaptation** where natural selection causes a shift in the mean phenotype in the population through increases in the frequency of adaptive alleles in response to local environmental conditions (Sanford and Kelley, 2011).

For corals, acclimatisation and adaptation can occur in the coral host or associated microbial partners (**Box 3**), a topic well explored in Torda *et al.*, 2017, van Oppen *et al.*, 2015, and Webster & Reusch, 2017.

The suites of delivery methods presented here are based on the principles of **human-assisted evolution.** This concept aims to accelerate naturally-occurring evolutionary processes such as acclimatisation or adaptation, to enhance particular traits of interest (Jones and Monaco, 2009; van Oppen *et al.*, 2015; **Box 3**) and has also been termed **facilitated adaptation** (Thomas *et al.*, 2013; Johnson *et al.*, 2016). Assisted evolution is based on biological engineering principles (including selective breeding, probiotics and genetic engineering), which are already successfully applied to improve human health and food production (van Oppen *et al.*, 2015) and are only just beginning to be explored in the field of biodiversity conservation (Piaggio *et al.*, 2017).

Box 3: What is acclimatisation and adaptation?

Acclimatisation involves **phenotypically** plastic responses in physiology, morphology, or behaviour that can help maintain or increase fitness in a new environment (Sunday et al 2014). Acclimatisation is reversible and does not involve a genetic change (although plasticity itself can have a genetic basis [Brown and Cossins 2011]). In corals, acclimatisation can occur through several pathways. Intra-generational acclimatisation can cause physiological adaptations within the lifespan of an individual, and may occur through stress memory, as well as epigenetics and nutritional factors (e.g. transfer maternal lipid reserves). Recent evidence suggests some non-genetic changes to phenotypes are heritable (i.e. trans-generational acclimatisation, reviewed in van Oppen et al 2015). Epigenetics can also influence the community of microbes associated with an organism, causing a phenotypic change in the host organism at the holobiont level (Webster and Reusch 2017). These changes can be passed onto the next generation.

In contrast, adaptation involves a genetic change in the form of allele frequency changes from one generation to the next, caused by natural selection on the phenotype (Sunday et al., 2014). When populations are diverse and harbour ample existing genetic diversity (i.e. standing genetic variation), this process can be relatively rapid (Torda et al., 2017).

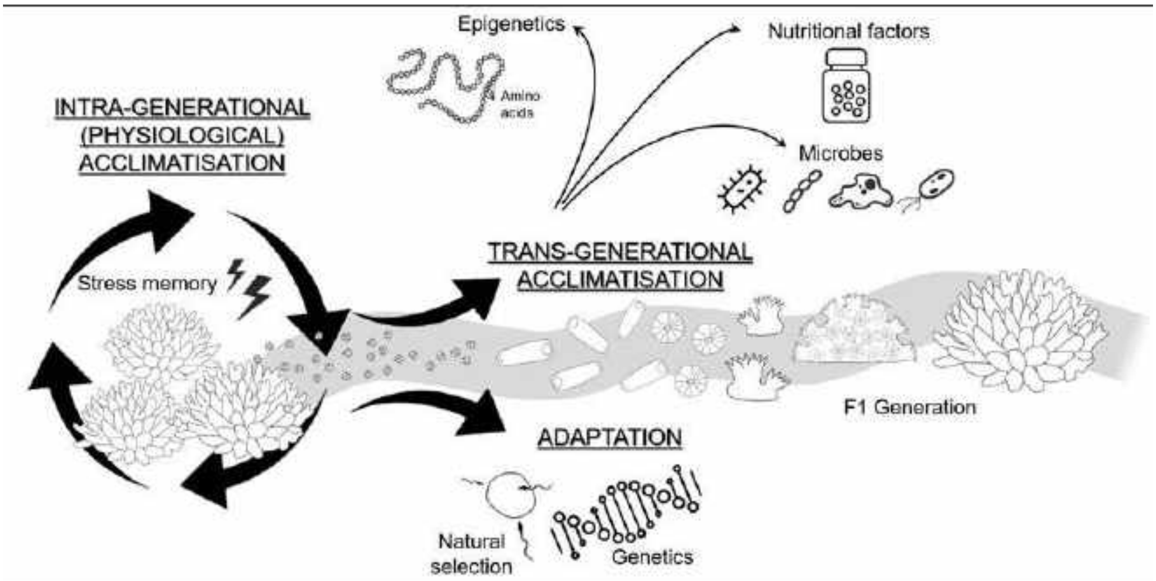


Figure modified from van Oppen et al 2015, Torda *et al.*, 2017, and Webster & Reusch, 2017.

Box 4. What is genetic diversity?

Genetic diversity describes variation in the genomes of organisms and is essential for maintaining survival by facilitating adaptation within populations in natural, changing environments (Vali *et al.*, 2008). The generation and maintenance of genetic diversity is dependent upon the processes of mutation, genetic drift, migration, and natural selection. There are two distinguishing types of genetic diversity: neutral and adaptive (also known as functional or selective) variation. Both neutral and adaptive diversity can occur on multiple levels within the coral holobiont (i.e. host animal, Symbiodiniaceae (symbiotic algae), and as well as bacteria, viruses and fungi). Standing genetic variation within a population is defined as genetic regions (**loci**) where there is a presence of more than one variant (**allele**).

Neutral diversity is the proportion of genetic diversity that has no effect on fitness. This type of variation is detected by most molecular-genetic laboratory techniques (e.g. microsatellites or single nucleotide polymorphisms (SNPs); (Holderegger *et al.*, 2006)). However, neutral genetic variation can provide extensive information for landscape ecology regarding gene flow, migration, and dispersal patterns (Holderegger *et al.*, 2006). Adaptive diversity refers the proportion of genetic variability that influences fitness and can be established through new, beneficial mutations, or recombination and redistribution of existing genetic variants (Messer and Petrov, 2013). Adaptive variation can be identified using quantitative trait loci (QTL). These loci (or markers) are associated with health and fitness benefits under prevailing environmental conditions. Adaptive, selective genetic diversity is more difficult to estimate compared with neutral diversity, and requires quantitative genetic designs (Holderegger *et al.*, 2006). Both estimates are needed to assess demographic processes (neutral diversity) and adaptive potentials (adaptive diversity).

Limited genetic diversity can constrain the adaptation of populations and decrease fitness in the short term (i.e. inbreeding depression; Vali *et al.*, 2008). Populations of some coral species often have high levels of standing genetic diversity (Matz *et al.,* 2018), which may be due in part to the occurrence of interspecific hybridisation across some taxa (van Oppen *et al.,*2015), and to a lack of segregation between **somatic cells and the germline**. Coral germ-line cells develop from somatic cells, which have been exposed to developmental and environmental cues throughout the individual's life (van Oppen *et al.,* 2011b). This provides a wider scope for epigenetic changes and somatic mutations to introduce genetic variability in coral populations (van Oppen *et al.,* 2015). Therefore, the amount of standing genetic diversity within populations can determine how fast they can adapt to rapid environmental change (Barrett and Schluter, 2008; Visser, 2008).

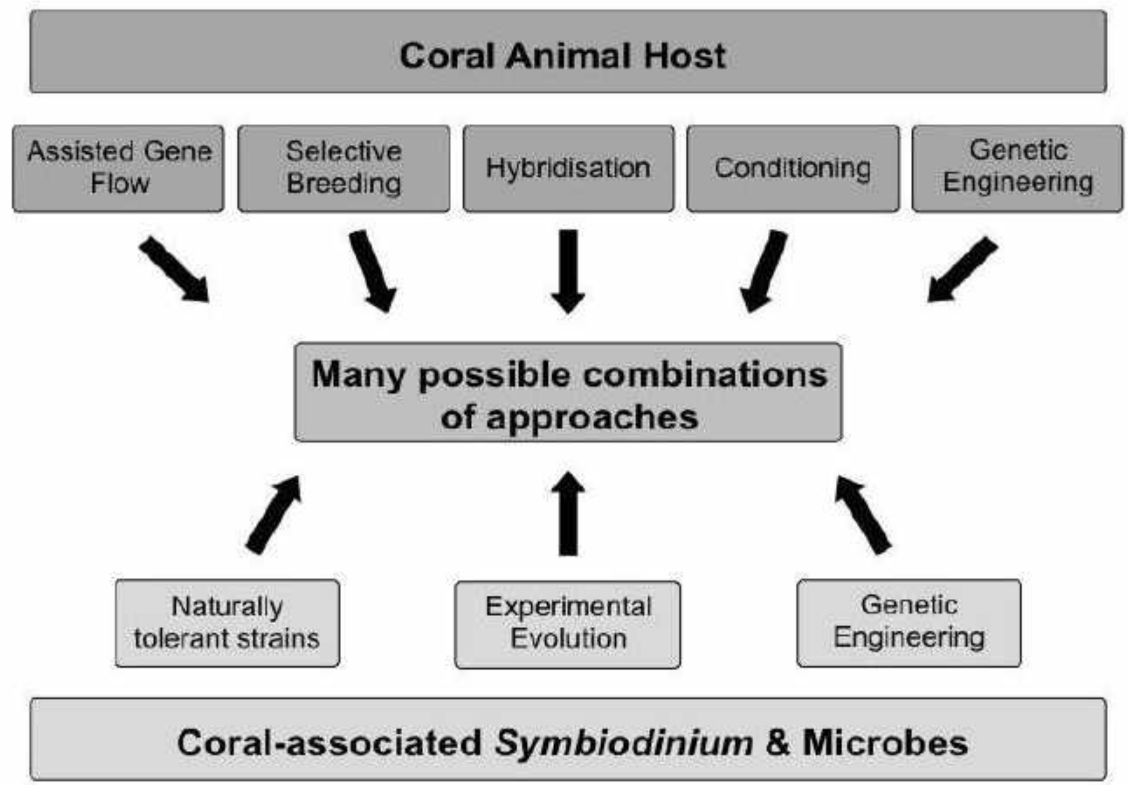


Figure 9: Diagram summarising the motivation for, and steps involved in, the eight assisted evolution approaches (i.e. delivery methods) discussed. Modified with permission from van Oppen et al., 2015.

4.2.1 Enhanced tolerance via interbreeding of existing coral genetic stock

One proposed delivery method aims to enhance the stress tolerance of corals on the Great Barrier Reef is via genetic **introgression**, where new genetic variation for stress tolerance is incorporated into a receiving population by interbreeding with tolerant individuals from another (differentiated) reef population (from within or outside the Great Barrier Reef) or a different species (Petit and Excoffier, 2009; Ellegren and Galtier, 2016; Chan *et al*., 2018). There are several intervention delivery methods that focus on the coral host animal that could facilitate this outcome (Figure 10 and 11). These include assisted gene flow, assisted migration, or colonisation, interspecific hybridisation and marker-assisted selective breeding (Aitken and Whitlock 2013, van Oppen *et al*., 2015, 2017). The feasibility of these approaches is based on three major assumptions:

- The existence of relevant standing (i.e. existing) adaptive genetic variation within populations or species
- The absence and/or manageable level of unintended fitness consequences of hybrid individuals
- The presence of diagnostic genetic or environmental data to identify individuals and locations with adaptive diversity of interest.

The current state of knowledge around the benefits and risks for each delivery method are described in turn. The non-exhaustive list of risks associated with moving and breeding populations or species that would otherwise not reproduce (or reproduce very rarely) also include:

- Outbreeding depression, where offspring exhibit lower fitness than parents due to a lack of adaptation to either parental habitat in intermediate phenotypes
- Genetic bottlenecks, if the pool of individuals used for breeding is not sufficiently large to maintain genetic diversity
- Introductions of pests and diseases
- Altered ecological interactions including invasiveness.

Further genetic risks are discussed in Aitken and Whitlock 2013.

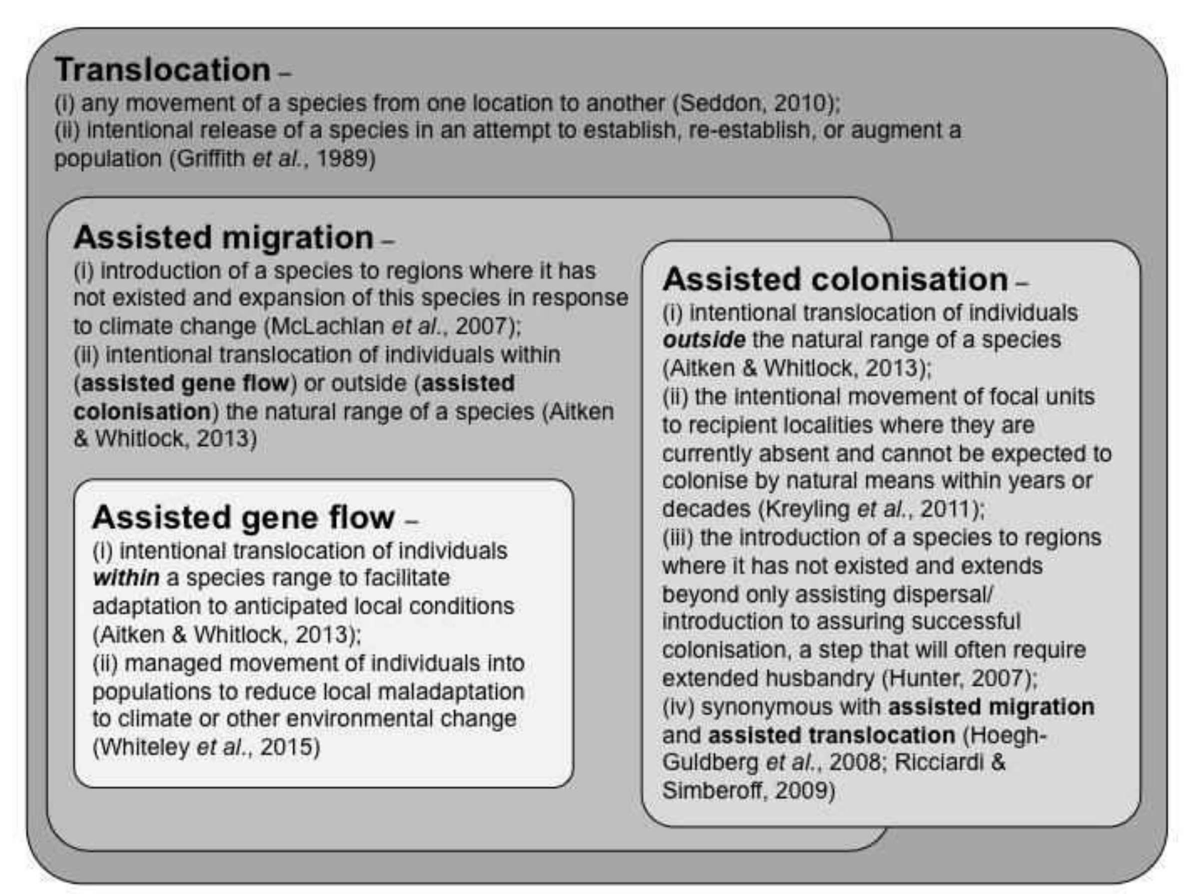


Figure 10: Terms used to describe approaches that introduce genes or species into receiving populations, and clarification of nomenclature used here in relation to the terms associated with the [movement of organisms for biodiversity conservation.](#) Please also see the glossary in [Appendix B.](#)

Assisted gene flow within the Great Barrier Reef

Assisted gene flow is the human-facilitated movement of individuals within a species to promote the rate of adaptation of populations to changing or future predicted environmental conditions (Aitken and Whitlock, 2013; Whiteley *et al.*, 2015). Considerable spatial variation exists in the temperatures that induce coral bleaching and mortality, which provides evidence that coral symbioses are adapted to local thermal environments (e.g. Coles *et al.*, 1976; Berkelmans, 2002; Riegl *et al.*, 2011). Coral populations harbour extensive standing genetic variation that may facilitate heat acclimatisation and/or adaptation (Matz *et al.*, 2018; Underwood *et al.*, 2018), and mass bleaching events may select for increased heat tolerance in surviving colonies (Hughes *et al.*, 2018b). It is unclear how the genetic diversity of populations might be affected under climate scenarios and increasing disturbance.

Assisted gene flow is proposed on the Great Barrier Reef as a mechanism to introgress naturally occurring, heat-tolerant genetic variation into other coral populations within the Reef. Introducing corals from, for example, northern regions, generally exposed to higher temperatures (and potentially those that have survived and recovered from recent bleaching events), to populations in cooler but warming locations, may provide novel genetic variation and increase the heat tolerance of reef populations in the future (provided that introduced individuals interbreed with native individuals) (Matz et al 2018; Quigley et al 2019). This can be achieved *in situ* through translocation of heat-tolerant corals to novel environments, followed by natural asexual propagation (i.e. fragmentation and growth), as well as sexual reproduction between the novel and local, native coral populations. *Ex situ* breeding, between colonies from either pure donor populations (e.g. thermally-tolerant parental colonies) or mixed with the receiving population (e.g. one thermally-tolerant parental **colony** and one receiving population parental colony), followed by deployment of the regional hybrid larvae or early juveniles onto the cooler reef is a scalable option and may reduce collection impacts on donor reefs. It may also be more successful if hybrids have thermal tolerance alleles (acquired from the thermally tolerant parent) within a genetic background optimised to local environmental conditions through longer-term natural adaptation (from native parent). Further, these early life stages have a greater potential to acclimatise to local conditions via developmental acclimatisation (Munday *et al.*, 2013) than translocated adult fragments.

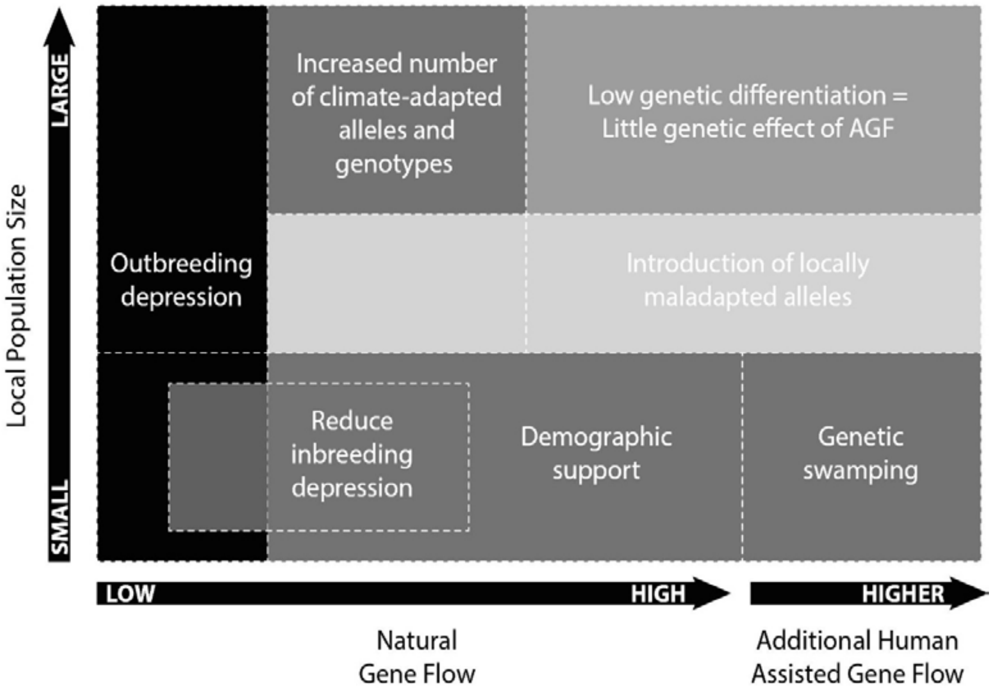
Heat tolerance tests on laboratory-bred corals found that **F1** (first generation) larvae have higher thermal tolerances, at least if the mother originated from a warmer reef (Dixon *et al.*, 2015). Field studies suggest that F1 regional hybrid juveniles survive better than introduced F1 purebred juveniles but die more than purebred local corals (van Oppen *et al.*, 2014). When crossing northern and central populations followed by transplantation to a central reef there were no negative effects on larval survival, weight and settlement, and juvenile survival (Quigley *et al.*, 2016). While these early studies are promising, further examination is needed to fully assess potential negative impacts, including: the loss of fitness due to a break-up of co-adapted gene complexes or the creation of negative interactions of the novel variants with the local environment (Baums, 2008); the unintentional dilution or disruption of locally-adapted or co-adapted alleles of other genes (Thomas *et al.*, 2013); and the rapid increase in frequency of introduced non-adaptive variants that leads to substantial replacement of local variants due to a numerical or fitness advantage (**gene swamping**; Hufford and Mazer, 2003).

Rigorous and extensive testing is dependent on juvenile and adult coral husbandry, aquaculture breeding techniques, and the spread of novel and beneficial genetic variants in receiving populations. Approaches to large-scale coral husbandry and propagation will be addressed in the

R&D plan for the Enhanced Corals, Treatments and Aquaculture Subprogram. The genetic interactions between novel and local populations are currently also being modelled (Matz et al 2018, Quigley et al 2019).

Assisted migration from outside the Reef, or introduction of new species

Assisted migration describes the intentional movement of individuals to recipient localities outside their natural distributional range (Aitken and Whitlock, 2013), or where they cannot be expected to colonise by natural means within years or decades (also referred to as assisted colonisation, managed translocation and managed relocation; Kreyling *et al.*, 2011). It can also be applied at the community level through the introduction of new species. This latter strategy is most commonly considered a 'Noah's Ark' approach to protect threatened species or populations by moving them to refugia not exposed to the damaging conditions, and assuring successful colonisation with an additional step of extended husbandry (Hunter, 2007; a process termed



assisted colonisation).

Figure 11: Potential positive and negative effects of assisted gene flow in corals on the Great Barrier Reef. Assisted gene flow involves human-assisted movement of individuals within a species, to facilitate the adaptation of populations to future conditions. Redrawn with permission from Aitken and Whitlock, 2013.

For corals on the Great Barrier Reef, assisted migration of genes from outside the Reef could be used to introduce beneficial variation from the source population into the receiving population(s). It has been proposed to introduce coral individuals or species from the Coral Triangle or the Persian Gulf where they grow and survive under higher ambient temperature regimes than those currently experienced on the Great Barrier Reef (Hoegh-Guldberg *et al.*, 2008; Coles and Riegl, 2013). Corals in the Persian Gulf, for example, are consistently exposed to temperatures 3 – 7°C higher than in other parts of the world (Riegl *et al.*, 2011), and, consequently, have higher thermal tolerance (Howells *et al.*, 2016). With continued rising sea temperatures and the reoccurrence of severe bleaching events in the Persian Gulf (Coles and Riegl, 2013), it has been suggested that assisted colonisation of threatened Persian Gulf corals should be considered to ensure the protection of their genetic legacy. These species represent 10 percent of the common Indo-Pacific coral fauna and hence also provide a heat-resistant reservoir of corals for the world.

Many arguments exist against assisted migration, ranging from adverse effects on ecosystem composition and functioning (e.g. creating biased flora/fauna, disturbing nutrient cycling and productivity) to technical feasibility and lack of predictive/informative risk assessments (Hoegh-Guldberg *et al*., 2008; Pelini *et al.*, 2009; Ricciardi and Simberloff, 2009; Kreyling *et al.,* 2011). While these counter arguments are legitimate concerns, they should be assessed and addressed in the context of other risks (e.g. extinction due to climate change) in risk and decision-making frameworks (Riegl *et al.*, 2011). In comparing assisted gene flow, assisted migration, and assisted colonisation, assisted gene flow may have lower ecological risks (as the focal species is already present) and higher genetics risks (outbreeding depression and genetic swamping; Aitken & Whitlock, 2013; **Figure 12**). It should be noted that assisted migration could be considered as a final resort.

Marker-assisted selective breeding

Marker-assisted selective breeding uses genetic markers to select brood stock that have the desired phenotype – such as heat tolerance, growth rate or other (Rothschild and Ruvinsky, 2007; Abdelrahman *et al.*, 2017). This method has been developed and extensively and applied in aquaculture for food production over the past decade (e.g. Rothschild and Ruvinsky, 2007; Yue, 2014; Abdelrahman *et al.*, 2017) and has the potential to support breeding for restoration and adaptation (Rau *et al.*, 2012; Guest *et al.*, 2014; van Oppen *et al.*, 2017). Phenotypic variation in traits, such as growth or thermal tolerance, is typically associated with quantitative variation at any number of genetic loci (also known as **quantitative trait loci [QTLs]**, Box 4). QTLs can be identified with **SNPs** (single nucleotide polymorphisms) or **AFLPs** (amplified fragment length polymorphisms) and are essential for understanding the molecular mechanisms underpinning phenotypes (Abdelrahman *et al.*, 2017). The use of QTLs for aquaculture of other species, particularly invertebrates, provide promise for use in corals. In the Pacific oyster (*Crassostrea gigas*), growth (Guo *et al.*, 2012), resistance against summer mortality (Sauvage *et al.*, 2010), and viability (Plough and Hedgecock, 2011; Plough *et al.*, 2016), have been linked to QTLs. However, nominated traits in selective breeding (i.e. thermal tolerance) may have differential, and potentially opposite, effects on the organism, dependent upon the life stage. For example, in Sydney rock oysters (*Saccostrea glomerata*), up-regulation of specific cellular systems increased tolerance to elevated CO_2 and was beneficial for larvae, however this was subsequently detrimental to adult oysters (Thompson *et al.*, 2015).

In addition to marker-assisted selective breeding, brood stock can also be chosen based on the coral phenotype, or the local environment to which they have likely adapted. Interbreeding of corals from different regions on the Great Barrier Reef found variation in offspring fitness (van Oppen *et al.*, 2014, Quigley *et al.*, 2016). Additional research is needed to explore multiple and additional trait responses and the effects and outcomes of breeding in future generations (**F2, F3**, etc.) and breeding potentials of different species. Currently, selective breeding of survivors from recent bleaching events attempts to test whether natural selection has selected for individuals with enhanced thermal tolerance.

Box 5: What are quantitative trait loci (QTLs)?

Acropora millepora is a well-characterized model species Image Credit: Allison Paley James Cook Univeristy

Specific QTLs in corals have been identified with regards to bleaching tolerance and antioxidant capacity (Lundgren *et al.*, 2013; Bay and Palumbi, 2014; Dixon *et al.,* 2015; Jin *et al.,* 2016). *β-hexosaminidase* and *Elongation factor 1-α*, in *Pocillopora damicornis,* significantly correlated with temperature in *P. damicornis* type α and with temperature and water clarity in *P. damicornis* type β (Lundgren *et al.*, 2013). In *Acropora millepora, Ligand of Numb X2* and *Thioredoxin* SNPs correlated with water clarity, while *β-gamma crystallin*, *Galaxin*, and *Ubiquitin* SNPs correlated with temperature (Lundgren *et al.*, 2013). Additionally, in *Acropora millepora*, heat-tolerant larvae were associated with the upregulation of genes relating to oxidoreductase activity and extracellular matrix, and downregulation of genes associated with transmembrane transport and motor activity (Dixon *et al.*, 2015). Two SNPs (*C29226S281* and *C70S236*) have also been identified and suggested as true QTLs in *A. millepora* for higher antioxidant capacity, thermal tolerance, and water quality tolerance (Jin *et al.*, 2016).

Interspecific hybridisation for novel genomics

Introgressive hybridisation of species (inter-specific) or differentiated populations (intra-specific; **4.2.1 Assisted gene flow** and **4.2.1 Assisted migration** considered above) can produce novel genomic combinations, and facilitate adaptation to changing or disturbed environmental conditions (Rhymer and Simberloff, 1996). The generation of novel genomic combinations can result in transgressive hybridisation (creation of hybrids with more extreme phenotypes than their parental lines; Whiteley *et al.*, 2015) and can increase **hybrid vigor**, a condition where offspring enjoy higher fitness than their parents (Shull, 1948). Hybridisation may be relatively common in animal and plant species and occurs in both terrestrial and marine environments (reviewed in Arnold, 1992; Dowling and Secor, 1997; Gardner, 1997; Mallet, 2005; Willis *et al.,* 2006).

Interspecific hybridisation is believed to play a major role in the evolution of coral species (Willis *et al.,* 2006) and can occur naturally among some coral species (Fogarty, 2012). Hybrids between certain species can also be created through single choice laboratory experiments (Willis *et al.,* 1997, Isomura *et al.,* 2016, Chan *et al.*, 2018, 2019). There is some evidence for increased fitness of hybrids compared with their parents. For example, *A. prolifera*, the natural hybrid between the Caribbean species *Acropora palmata* and *A. cervicornis*, has equivalent or higher fitness relative to its parent species, and has increased its distribution and abundance despite recent degradation of the reefs where it occurs (Fogarty, 2012). Laboratory-produced *Acropora* hybrids of the F1 generation from the Great Barrier Reef grew faster than their parents in some reef environments (Willis *et al.,* 2006) and had higher fitness related traits (i.e. growth and survival under laboratory-based elevated temperature and CO_2), relative to at least one parent (Chan *et al.*, 2018). It is important for future breeding experiments to assess whether F1 hybrids (and generations beyond) are able to reproduce sexually, as hybrids are often found to be sterile (Vollmer and Palumbi, 2002; Flot *et al.*, 2011; Wei *et al.*, 2012, but see Richards and Hobbs, 2015). In fertile hybrids later generations can show **outbreeding depression**, the consequences of which can be as significant as inbreeding depression (Edmands, 2007). In long-lived coral hybrids, this intervention delivery method may be beneficial to coral reef resilience even if sexual reproduction is absent.

Conditioning

Inducing a shift in the stress tolerance of an organism due to sub-lethal stress exposure is known as **conditioning** or **stress hardening.** This process allows organisms to acclimatise, and potentially adapt, to changes in their environment. This acclimatisation can be within generations (physiological acclimatisation of the individual through stress memory) and reversible or passed between generations (**transgenerational acclimatisation/plasticity** through potential mechanisms, including epigenetic programming; TGP; Torda *et al.*, 2017).

Physiological acclimatisation of corals has been extensively studied and reviewed (e.g. Weis, 2010); however, due in part to the long generation times (Babcock, 1991; van Oppen *et al.,* 2011a), and complex reproductive methods (Baird *et al.*, 2009), transgenerational plasticity is just beginning to be documented and studied in corals (e.g. Putnam & Gates, 2015; Torda *et al.*, 2017; Putnam *et al.*, *in review* (Biorxiv); Quigley et al., in review (Biorxiv)). This process provides a long-term increase in tolerance to climate change stressors through **epigenetic** changes (Putnam *et al.*, *in review* (Biorxiv); but also see **4.2.3 Enhanced tolerance via additional microbes** for microbe-mediated transgenerational acclimatisation). Epigenetic changes are external modifications of genes, without a change in the genetic sequence, that induces changes in expression level (i.e. DNA methylation, histone modifications, chromatin remodelling, noncoding and antisense RNAs; Handel *et al.*, 2010; Feil & Fraga, 2012; Torda *et al.,* 2017).

Transgenerational plasticity is currently being studied in many marine and model invertebrates (e.g. Sydney rock oyster, *Saccostrea glomerata* - Thompson *et al.*, 2015; Olympia oyster, *Ostrea lurida* - Hettinger *et al.*, 2012; model roundworm, *Caenorhabditis elegans* - Klosin *et al.*, 2017; model marine polychaete, *Ophryotrocha labronica* - Gibbin *et al.*, 2017), and some corals (e.g. *Acropora millepora* – Dixon *et al.,* 2018; *Platygyra daedalea* – Kirk et al 2018). The mechanisms of transgenerational plasticity are currently unclear as potential pathways include somatic, genetic, and epigenetic factors, as well as associated microbes (Torda *et al.*, 2017). It is therefore essential to clarify its role in corals (Putnam and Gates, 2015; Torda *et al.*, 2017; Putnam *et al.*, *in review* (Biorxiv); Quigley *et al., in review* (Biorxiv)). Future research should focus on demonstrating transgenerational plasticity in well-defined experiments, and understanding its relative genetic, epigenetic, and microbial contributions to future generations of corals. While rapid acclimatisation may occur naturally in populations exposed to sub-lethal temperature stress (e.g. Torda et al., 2017), current research is exploring whether it is possible to manually induce this shift in phenotypic performance. Therefore, physiological and transgenerational acclimatisations must be considered in reef restoration and adaptation programs.

4.2.2 Enhanced tolerance via symbiotic microalgae (family Symbiodiniaceae)

The endosymbiotic relationship established between corals and microalgae of the family Symbiodiniaceae is essential to their health and fitness and profoundly affects the ecology and evolution of both partners. Both the coral host and the symbionts benefit from the endosymbiotic relationship: coral hosts provide a microhabitat, protection, and nutritional requirements to their algal symbionts (Smith and Douglas, 1987; Trench, 1987), while the Symbiodiniaceae provide their hosts with the benefits of a primary producer, satisfying more than 90 percent of the energy requirements of some species (Trench, 1979; Muscatine, 1980; Muscatine, 1990). In this exchange, the algal symbiont can affect the growth, nutritional status, bleaching tolerance, and survival of its coral host (e.g. Rowan *et al.*, 1997; Little *et al.*, 2004; Berkelmans and van Oppen 2006; Abrego *et al.*, 2008; Cantin *et al.*, 2009; Bay *et al.*, 2009b). The translocation of photosynthates from Symbiodiniaceae is necessary for calcification (Barnes and Chalker, 1990). Light-enhanced calcification of corals is mediated by their algal symbionts through the elimination of excessive carbon dioxide and phosphate. These processes contribute to the massive calcium carbonate skeletal structures that are the foundation of coral reef ecosystems (Goreau and Goreau 1959; Simkiss 1964; Loh *et al.*, 2001).

Due to the functional and genetic diversity and their (general and specific) associations with coral host species (Trench, 1993), the high abundance in which they are found in coral host tissues (1-3 x 10^6 symbionts per cm^2 makes the genus Symbiodiniaceae a keystone species group that underpins the tolerance of corals, their adaptive potential and thus future health of coral reef ecosystems (Paine, 1969; Power *et al.*, 1996; Baker, 2003).

It has been proposed that evolution can occur much more quickly within the Symbiodiniaceae community compared with the coral host. As such, manipulating the Symbiodiniaceae communities may facilitate faster acclimatisation—and potentially adaptation to future climate conditions—within the coral host.

Manipulation of the Symbiodiniaceae community can be achieved through influencing the:

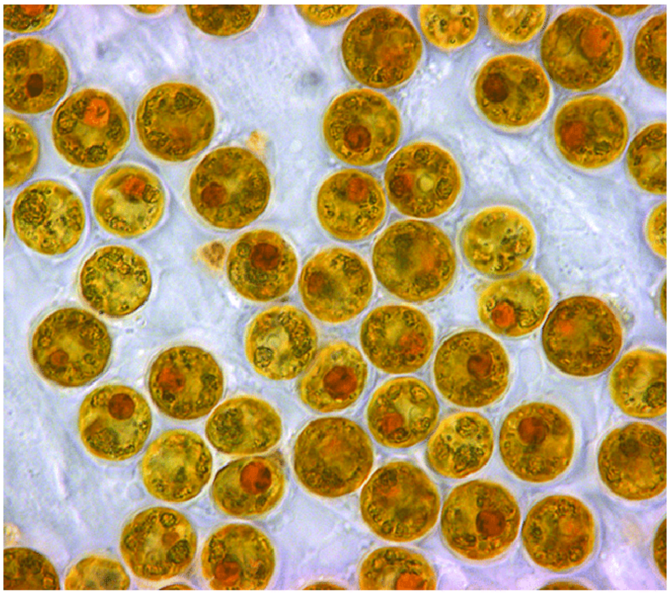
- Presence or abundance of existing Symbiodiniaceae within coral hosts
- Presence or abundance of experimental evolved or engineered Symbiodiniaceae
- Transgenerational conditioning through epigenetic reprogramming.

Box 6: What are Symbiodiniaceae?

Algal cells can be seen within the tissues of the coral polyp Image from https://phys.org/news/2013-07-coral-symbiont-genome-decoded.html

Symbiodiniaceae is a genetically- and physiologically-diverse family of microalgae, consisting of five genera with distinct geographic distributions among coral hosts and local environments. A recent systematic revision has reclassified the previous five *Symbiodinium* clades associated with scleractinian corals (A, B, C, D, and F), into five proposed new genera (*Symbiodinium, Breviolum, Cladocopium, Durusdinium and Fugacium* respectively; LaJeunesse et al 2018). These genera can be widely distributed (e.g. *Cladocopium* is found worldwide; Burnett, 2002; Loh *et al.*, 2001; Rodriguez-Lanetty and Hoegh-Guldberg 2003; Baker 2003; van Oppen *et al.*, 2009), while others have restricted distributions due to host or habitat specificity (e.g. *Fugacium* is restricted to the temperate western Pacific Ocean; Baillie *et al.*, 2000; Baker, 1999; LaJeunesse, 2001; 2002; LaJeunesse *et al.*, 2003; Santos *et al.*, 2003).

Geographically, there appears to be ocean basin specificit (Baker and Rowan, 1997; LaJeunesse *et al.*, 2003; Baker, 2003), as well as a latitudinal (i.e. tropical/temperate) divergence in Symbiodiniaceae distribution patterns (Baker, 1999; Rodriguez-Lanetty *et al.*, 2002; Savage *et al.*, 2002; Baker, 2003). *Symbiodinium and Breviolum* are dominant in the Caribbean, while *Cladocopium* dominates the Pacific. Additionally, genera can be depth stratified. *Symbiodinium, Breviolum,* and *Durusdinium* are found in shallow colonies of *Montastraea annularis* and *Montastraea faveolata*, whereas *Cladocopium* is found in deep water corals (within the Caribbean; Rowan and Knowlton, 1995; Rowan *et al.*, 1997; Toller *et al.*, 2001; Baker, 2003). However, *Montastraea franksi* harbours *Durusdinium* in deeper waters (Toller *et al.*, 2001; Baker, 2003). Depth stratification between symbiont types within *Cladocopium* was also observed on the Great Barrier Reef (Bongaerts *et al.*, 2010). Further, clades *Symbiodinium, Breviolum*, and *Fugacium* are more commonly associated with sub-tropical and temperate waters, while *Cladocopium* is predominantly tropical (Baker, 1999; Rodriguez-Lanetty *et al.*, 2002; Savage *et al.*, 2002; Baker, 2003). This indicates that temperature and light are important factors in determining geographical distribution patterns of Symbiodiniaceae species.



Isolated algal cells each ~ 10 micrometers. Image from Photo: TC. LaJeunesse, Penn State University.

Scleractinian corals obtain their symbiont partners by vertical, horizontal or mixed transmission. Vertical (direct) transmission occurs when eggs acquire symbionts directly from the parental colony (Trench 1987; Benayahu and Schleyer, 1998), prior to the release of eggs in some spawning coral species (Szmant *et al.*, 1980; Arai *et al.*, 1993; Schwarz *et al.*, 1999; Loh *et al.*, 2001) or during the period of larval brooding in others (Richmond 1981; Benayahu and Schleyer, 1998; Shlesinger *et al.*, 1998; Sier and Olive, 1998; Titlyanov *et al.*, 1998; Loh *et al.*, 2001). Vertical transmission equips the next generation of corals with similar presumably well-adapted, symbionts for a local environment although novel uptake can also occur (Quigley *et al.* 2018b).

Horizontal transmission occurs when corals acquire symbionts from the environment in the larval or post-larval phases (Trench, 1987). Horizontal transmission is the most common mode of Symbiodiniaceae acquisition in corals (Babcock *et al.*, 1986; Harrison and Wallace, 1990; Shlesinger and Loya, 1991), and approximately four times more common than vertical transmission in the dominant group of broadcast spawning corals (Baird *et al.*, 2009). For these coral species, symbionts are most likely acquired from free-living populations in reef sediments (Coffroth *et al.*, 2006; Adams *et al.*, 2009; Quigley et al 2017), expelled mucus from other corals (Hoegh-Guldberg *et al.*, 1987) and the water column (Manning and Gates 2008). Acquisition from the environment may promote flexibility and diversity in the Symbiodiniaceae genera and types hosted by corals (Douglas, 1998; Baird *et al.*, 2007; Dunn and Weis, 2009).

Manipulate abundance of existing Symbiodiniaceae *types*

The association between corals and Symbiodiniaceae, in abundance and type, is naturally flexible, as demonstrated by extreme events (e.g. bleaching – Baker *et al.*, 2002), as well as by acclimatisation to local environmental conditions (e.g. water quality – Rocker *et al.*, 2017). The presence and abundance of Symbiodiniaceae species/ type is important in determining stress resistance (i.e. thermal tolerance; Swain *et al.*, 2017; Cunning *et al.*, 2015b; Cunning and Baker, 2014). The coral host naturally mediates its symbiont communities in response to the surrounding environment, and therefore, manipulation of Symbiodiniaceae communities, through both abundance and type, could potentially be used to increase coral resilience to climate change.

The inoculation of corals with cultured naturally tolerant Symbiodiniaceae aims to increase the coral holobiont's thermal tolerance to future climate conditions. Symbiodiniaceae communities are naturally variable in thermal tolerance (Swain *et al.*, 2016; Gregoire *et al.*, 2017). There is a general consensus that *Symbiodinium* and *Durusdinium* are more thermally tolerant relative to *Breviolum* and *Cladocopium* (e.g. Swain *et al.*, 2017; Kemp *et al.*, 2015). This generalisation can be further influenced by source location, as symbionts from warmer reefs performed better (in terms of photochemical performance and survivorship) than symbionts from cooler reefs when exposed to thermal stress (both in culture and in symbiosis; Howells *et al.*, 2012). Further clarification is required as specific genotypes within genera may have substantially different tolerance characteristics (Howells *et al.*, 2012). Additionally, as proportions of thermally tolerant Symbiodiniaceae communities increase in corals, and bleaching susceptibility decrease, trade-offs, including reduced photochemical efficiency (Cunning *et al.*, 2015a) and/or coral growth rates (Little *et al.*, 2004), may also occur.

Manipulate abundance of experimental evolved Symbiodiniaceae

Experimental evolution is the directed evolution of a population generally within a laboratory under specified conditions through multiple generations (Chakravarti et al. 2017). For Symbiodiniaceae populations (that have a high adaptive potential), experimental evolution is feasible due to large population sizes (~10^{10} cells in a branching coral ~30cm diameter; Drew, 1972; Littman *et al.*, 2008, van Oppen *et al.*, 2011b), genetic isolation (Santos *et al.*, 2003; Howells *et al.*, 2009) and short asexual generation times (3 - 74 days; Wilkerson *et al.*, 1988).

Few studies have explored the long-term response and evolution of Symbiodiniaceae to thermal stress (Huertas *et al.*, 2011; Chakravarti *et al.*, 2017, 2018). These studies find that, after at least 40 generations of experimental selection of Symbiodiniaceae strains, selected *Cladocopium* strains perform better compared with wild-type strains under thermal stress in culture. This improved performance has not yet translated to an improved *in-hospite* performance of multiple *Acropora* species (Chakravarti *et al.*, 2017, 2018) therefore, future research should focus on developing this increased thermal tolerance and its transference to the coral host.

Transgenerational conditioning through epigenetic reprograming

See section **4.2.1 Conditioning** for coral host transgenerational acclimatisation and **4.2.3 Enhanced tolerance via additional microbes** for microbe-mediated transgenerational acclimatisation.

By advancing current knowledge of coral-symbiont relationships, particularly the dynamics of endosymbiont acquisition in reef corals, supportive measures (e.g. induced acquisition of potentially environmentally tolerant Symbiodiniaceae) could be implemented to aid corals in their acclimative and/or adaptive responses.

Feasibility, potential risks, and knowledge gaps

Due to the complexity of initial acquisition, regulation, and potential re-acquisition post-bleaching (e.g. Weis, 2008; Davy *et al.*, 2012), many knowledge gaps regarding the molecular basis of coral and Symbiodiniaceae symbioses still exist. It is possible that model systems such as *Hydra* and *Aixaptasia* can be used to quickly uncover fundamental principles and generate hypotheses that can subsequently be tested in corals (Davy *et al.*, 2012). Risks associated with manipulating Symbiodiniaceae include potential tradeoffs between desirable traits selected for, and other known or unknown linked traits. For example, increased thermal tolerance in some species has been linked to reduced growth in coral hosts (Little et al., 2004, Jones et al., 2008). Further, the risk of introducing novel species on the Reef include invasiveness and altered symbiotic and ecological interactions.

4.2.3 Enhanced tolerance via additional microbes (prokaryotes, viruses, and/or fungi)

The coral animal lives in close association with microbial communities defined as the coral **microbiome**. This includes Symbiodiniaceae (considered separately in **4.2.2. Enhanced tolerance via symbiotic microalgae (family Symbiodiniaceae),** bacteria, archaea, protists, fungi and viruses (Rosenberg *et al.*, 2007; Ainsworth *et al.*, 2010; Bourne *et al.*, 2016). The functional basis for these microbial symbioses primarily centres on cycling of essential nutrients such as carbon, nitrogen, sulphur, and phosphate, as well as passage of trace metals, vitamin synthesis, provision of cofactors, and production of secondary metabolites (reviewed in Bourne *et al.,* 2016).

The microbial community of corals and their associated functions can be altered by changes in the health status of the holobiont (Sweet and Bythell, 2017) as well as changes in environmental conditions including elevated sea surface temperatures and ocean acidification. For example, alterations in microbial communities have been found to occur during field bleaching events (Bourne *et al.,* 2008; Littman *et al.,* 2011) and in response to elevated temperature (Vega Thurber *et al.,* 2009; Webster *et al.,* 2016; Liang *et al.,* 2017; Ziegler *et al.,* 2017), pH changes (Vega Thurber *et al.,* 2009; Meron *et al.,* 2011; Bell *et al.,* 2013), and nutrient enrichment (Vega Thurber *et al.,* 2009, 2014). These environmentally induced changes in the microbiome highlight the importance of further understanding the microbiome and how different aspects of the holobiont interact with each other and the environment (Hernandez-Agreda *et al.,* 2017). Recently, the National Science Foundation and 23 additional US Government agencies invested in planning and funding microbiome research (**The Interagency Strategic Plan for Microbiome Research**), including interdisciplinary research to facilitate understanding of microbiome functioning in diverse ecosystems (including coral reefs).

The microbial community has larger diversity and population sizes, significantly shorter generation times and a large metabolic range compared with the coral host (Elena and Lenski, 2003; Torda *et al*., 2017). It has therefore been proposed that evolution can occur through **microbiome-mediated transgenerational acclimatisation** (Webster and Reusch, 2017) in addition to adaptation of the coral host. (See **Conditioning section for transgenerational acclimatisation**). Research using the model organisms *Nematostella vectensis* (Mortzfeld *et al*., 2016) and *Exaiptasis pallida* (Alagely *et al*., 2011) indicates that microbial partners are essential to acclimatisation and maintenance of homeostasis under changing environmental conditions.

Manipulation of the microbial community can be achieved through:

- Altering the abundance or ratios of existing microbes within the microbiome
- Adding novel, naturally beneficial (or probiotic) types of microbes
- Experimental selection of microbes.

Probiotics, also known as **beneficial microorganisms for corals** (Peixoto *et al.,* 2017), are bacteria, algae, fungi or viruses that could confer health benefits to the coral host or the Symbiodiniaceae. Some coral-associated microbial partners can be cultured without their host (Marx 2016; Röthig *et al.,* 2016), suggesting that production of probiotic microbial cocktails may be possible. Recently, coral larvae inoculated with a single dose of bacterial cocktail were shown to develop different microbiomes depending on the inoculum (Damjanovic *et al.,* 2017), supporting the hypothesis that the coral microbiome can be manipulated. Adult corals have also been inoculated with microbial communities that confer beneficial qualities, to enhance survival of the holobiont when exposed to environmental stress (dos Santos *et al.,* 2015). However, despite the potential for probiotics to enhance coral health and environmental tolerance, the mechanisms through which environmentally induced microbial alterations affect the functioning and acclimatisation/adaptation potential of the coral host are unknown. Further studies are required to fully address whether microbiome-mediated transgenerational acclimatisation (through symbiont changes or genetic evolution of the microbe) is possible in corals. Most importantly, it will be essential to determine whether any alterations to the microbiome can be maintained by vertical transmission of symbionts across generations, as ultimately this would be required for adaptation of the holobiont (Webster and Reusch 2017).

Manipulating abundance or ratios of existing microbes

Coral-associated microbes appear to provide a range of benefits to the coral host, although the mechanisms are not yet fully understood (**Table 1**; Peixoto *et al.,* 2017). For example, bacteria associated with the coral *Mussismilia hartii*, were selected for their ability to degrade water-soluble oil fractions, then re-applied as a probiotic, which minimised the effects of water-soluble oil fractions on coral health (dos Santos *et al.,* 2015). Cultivation of a diversity of coral-associated microorganisms would facilitate direct testing of their potential to support coral health in environmental and laboratory-simulated stress (Peixoto *et al.,* 2017). This approach may be applied to heat stressed corals with microbes that produce antioxidants in order to reduce oxidative stress, with compounds such as superoxide dismutases and lysozymes (Peixoto *et al.,* 2017).

Table 1: Examples of proposed probiotics (or BMCs). Reproduced unchanged from Peixoto et al., 2017.

Proposed beneficial characteristic	Beneficial mechanism	References
Photosynthesis	Input of organic compounds to the holobiont	Verbruggen and Tribollet, 2011; Burriesci *et al.*, 2012; Davy *et al.*, 2012; Tremblay *et al.*, 2012
Nitrogen fixation	Input of fixed nitrogen to the holobiont	Olson *et al.*, 2009; Lema *et al.*, 2012; dos Santos *et al.*, 2014; Bednarz *et al.*, 2015; Cardini *et al.*, 2015
Fixed nitrogen and carbon cycling and regulation	Control of organic compound distribution	Kimes *et al.*, 2010
Production of dimethylsulfoniopropionate (DMSP)	Bacterial populations control on the coral surface	Barott and Rohwer, 2012
Degradation of dimethylsulfoniopropionate (DMSP)	Increase carbon and sulfur availability; production of sulfur-based antimicrobial compounds such as tropodithietic acid (TDA)	Kirkwood *et al.*, 2010; Raina *et al.*, 2016
Production of mediated signals to larval settlement facilitation	Contribute to larval settlement modulation or regulation	Webster *et al.*, 2004; Heyward and Negri, 2010; Ritson-Williams *et al.*, 2010; Shikuma *et al.*, 2014
Production of antibiotics and competition with pathogens	Biological control of pathogens	Ritchie, 2006; Gochfeld and Aeby, 2008; Kirkwood *et al.*, 2010; Alagely *et al.*, 2011; Kvennefors *et al.*, 2012
Production of quorum sensing (QS) signal molecules, such as N-acylhomoserine lactones (AHLs)	Allow microbial interactions within the holobiont; can act on bacterial colonisation control, bioluminescence, pathogenesis control and extracellular enzyme production	Henke and Bassler, 2004; Ng and Bassler, 2009; Tait *et al.*, 2010; Sharp and Ritchie, 2012; Certner and Vollmer, 2015; Meyer *et al.*, 2015

Mechanisms influencing the protection of skeletogenic cells	Enhance the survival of skeletogenic cell types	Domart-Coulon *et al.*, 2004
Production of mycosporine-like amino acids (MAA)	Protection of coral tissue against ultraviolet radiation	Dunlap and Shick, 1998

Addition of novel, naturally beneficial (or probiotic) types of microbes

See **5.2.2 Antioxidant/anti-microbial biological systems**

Experimental selection of microbes

Enhancing beneficial traits of the coral microbiome presents new possibilities for coral holobiont acclimatisation and adaptation to future conditions. Probiotics for corals can be created through exposure to selection pressures in controlled, laboratory conditions (e.g. simulated heat stress; Damjanovic *et al.*, 2017). As such, microbes may adapt to continuous heat stress by increasing their antioxidant capacity and could then be applied as probiotics to corals (Damjanovic *et al.*, 2017).

Feasibility, potential risks, and knowledge gaps

Technical challenges associated with genomic and transcriptomic sequencing of coral-associated microorganisms has greatly hindered our understanding of microbial function in the coral holobiont (particularly relative to other model systems where the microbiome is generally much easier to sequence). These fundamental knowledge gaps pertaining to microbial function make it difficult to select target organisms for microbiome manipulation or the application of probiotics. Importantly, it still needs to be validated whether cultivated coral-associated microbes perform the same in culture as they do *in hospite.* It is also not known to what extent manipulating the coral microbiome may adversely affect corals or other reef organisms. As probiotic treatments are generally applied in closed systems (e.g. the treatment of *Clostridium difficile* infections in humans with faecal transplants; Kassam *et al.,* 2013), application of microbial manipulations in open systems, such as coral reefs, will prove extremely challenging. As microorganisms commonly found on coral reefs are frequently shared among many reef species, the introduction of manipulated microbes may trigger cascade effects to non-target species. Importantly, there is limited understanding of the symbiont acquisition strategies of most coral species (whether microbial symbionts are passed strictly vertically from parent to offspring or acquired horizontally from the environment in each new generation). If artificial manipulation of the microbiome is to offer a lasting mechanism for enhanced holobiont tolerance, it would be preferable to target vertically transmitted symbionts so that they are maintained within the host.

In terms of delivering probiotics to corals, inoculation of adult and juvenile corals with microbes during stressful periods, and during the recovery phase, has been proposed for both prevention and repair (Peixoto *et al.,* 2017). For instance, a single exposure of one coral to mucus sourced from another coral can direct the development of its subsequent microbiome (Damjanovic *et al.,* 2017). The delivery of microbial manipulations may be achieved through several methods, including the use of *ex situ* rearing in aquaria facilities (Damjanovic *et al.,* 2017), custom designed underwater robots, and incubation bags to ensure effective dilutions and exposure times of corals to the probiotic cocktail. While these methods can be applied at small spatial scales, it would be extremely challenging to apply at scale, since delivery methods are labour intensive and probiotics would have to be grown in large quantities. A potential horizontal infection of probiotics from a manipulated coral to neighbouring corals may increase the feasibility of applying probiotics at large scales, but this also comes with environmental risks associated with exposure of non-target species. It has also not yet been demonstrated that microbiome manipulation through the application of probiotics forms a stable, enduring association. If a stable partnership is not formed with the applied probiotic, then continual re-application would be required (as occurs in the application of most probiotics in aquaculture).

4.2.4 Genetic engineering or synthetic biology to enhance tolerance of coral holobiont

Changes in the genetic information (or **mutagenesis**) of the coral host, its Symbiodiniaceae, and/or associated microbes, may occur spontaneously in nature, be promoted by mutagen exposure, or be experimentally-induced in the laboratory (as outlined in sections on experimental evolution above). As such, novel mutations can be harnessed to offer additional approaches to enhance the coral holobiont through genetic changes of the coral host or its microbes. **Genetic engineering** is the application of technologies that permit direct manipulation of hereditary genetic material to alter a phenotype of interest in a target organism (Piaggio *et al.*, 2017). This genetic engineering approach has been extremely successful in improving agricultural crops, mass-producing compounds for industry, and in improving drug production. However, genetic engineering has not been possible for most ecologically relevant organisms, such as corals, because of the lack of technology allowing for genetic manipulation. In fact, the ability to genetically engineer organisms has been limited to a few, well-studied and taxonomically restricted groups, with specific biology that has made them genetically tractable. In recent years, this limitation of genetic engineering has been overcome with the discovery of new technologies, such as CRISPR/Cas9, that have enabled genetic manipulations in a wide variety of organisms. These new technologies have spurred the formation of an emerging area of research called **synthetic biology'** (Piaggio *et al.*, 2017).

Enhanced tolerance from genetic engineering with CRISPR/Cas9

With the advent of CRISPR/Cas9 technology, genetic engineering as a biodiversity conservation tool, specifically for reef corals, should be considered. **CRISPR/Cas9** is a biochemical method using clustered, regularly interspaced, short palindromic repeats (CRISPR) 'guide RNA' in conjunction with Cas9 (CRISPR-associated 9) nuclease, to efficiently cut and edit DNA containing the guide RNA sequence in the genome of the target organism (**Figure 13**; Esvelt *et al.*, 2014; Piaggio *et al.*, 2017). This technology allows the precise manipulation of target DNA in organisms including corals that affect phenotypes of interests, such as thermal tolerance. The technique can be used to both down- or up-regulate the expression of target traits.

The ability to introduce genetically engineered corals on the scale of the Great Barrier Reef is difficult without mechanisms to spread the engineered alleles. **Gene drives** are DNA pieces that are inherited more frequently than normal. Most DNA sequences in sexually-reproducing organisms have a 50 percent chance of being inherited by each offspring but the technique called gene drives changes this so that they are inherited more frequently (more than 50 percent chance; **more information here**). Thus, gene drives can spread selected, usually recombinant, DNA sequences (genes) through wild populations, with the aim of eliminating unwanted or adding desired characteristics (Kaebnick *et al.*, 2016; Piaggio *et al.*, 2017). The prospects of gene drives have been recognised for some time, but its application was limited by our ability to cut and edit DNA. However, combined with CRISPR/Cas9, gene drives are a promising new tool to efficiently spread selected genes throughout a population.

Recently, genome editing using the CRISPR/Cas9 tool was used to induce mutations in FGF1a (*encoding fibroblast growth factor 1a*), GFP (*green fluorescent protein*), and RFP (*red fluorescent protein*) the coral *Acropora millepora* by microinjecting single-guide RNA/Cas9 complexes into coral embryos (Cleves *et al.*, 2018). This method has also been used successfully in the model organisms *Nematostella vectensis* and *Hydractinia echinata* (Ikmi *et al.*, 2014; Servetnick *et al.*, 2017; Gahan *et al.*, 2017). By using reverse genetics (analysing the phenotypic effects of engineered gene sequences) and the CRISPR/Cas9 tool the functions of genes and pathways can be further examined in corals to determine, and potentially edit, their stress tolerance to climate change, and other phenotypes.

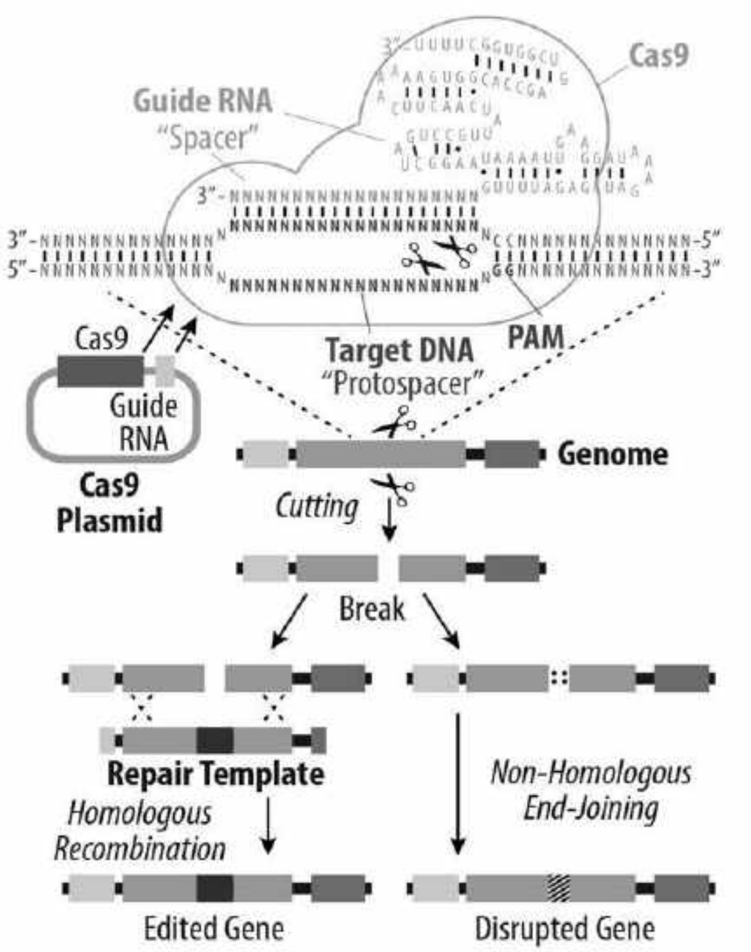


Figure 12: RNA-guided genome editing uses clustered regularly interspaced short palindromic repeats (CRISPR), guide RNA and Cas9 (CRISPR-associated 9) nuclease to cut and edit DNA containing the guide RNA sequence. Redrawn with permission from Esvelt *et al.,* 2014

Genetic engineering tools can also be applied to corals' symbiotic partners. Next generation sequencing has revealed many genetic elements that can potentially be engineered but also obstacles for success in Symbiodiniaceae spp. (reviewed in Levin *et al.*, 2017b). Recent work has generated Symbiodiniaceae protoplasts (viable cells with cell walls removed), which can facilitate modification of the nucleic material by genetic engineering (Levin et al. 2017a). Potential candidate genes to be targeted for genetic engineering (i.e. Fe-sod, Mn-sod, Prxd, and Hsp70) are predicted to enhance thermal tolerance and reduce bleaching (Levin *et al.*, 2016; Gierz *et al.*, 2017; Goyen *et al.*, 2017).

Additional technologies such as multiplex automated genome engineering (MAGE) can allow for large-scale programing, and accelerated evolution of cells, to find interacting mutations that synergistically produce beneficial phenotypes (Wang *et al.*, 2009). However, current MAGE technologies are in early stages of development and have been used exclusively in *E. coli*. Once transformation technologies are established, this type of technology may be able to be applied to Symbiodiniaceae or other associated microbes.

Recently developed technologies and knowledge for corals open up possibilities to enhance beneficial traits of the coral microbiome. For example, existing genes in the the coral microbiome can be manipulated with CRISPR-Cas9 (Tian *et al.,* 2017), and thus, it may be possible to alter the microbe's antioxidant capacity and increase its benefits to the coral during heat stress. In synthetic biology, a novel microbe with enhanced characteristics can be created with the introduction of new molecular pathways through artificially synthesised genetic material (Benner and Sismour 2005). A microbe might be constructed that can localise oxidative stress, invade cells, and produce targeted antioxidant compounds, such as superoxide dismutases, to help the coral survive heat stress (Peixoto *et al.,* 2017). These concepts could be used to produce microbes that can be applied as coral probiotics during heat stress.

Genetic manipulation of the coral, or its associated microbes, and subsequent release into the ecosystem is not without obvious environmental risks. For example, the introduction of mutations into the wild using gene drives has considerable unknowns that must be carefully considered and approved by all stakeholders before proceeding. However, advancing genetic engineering technologies will continue to provide valuable information about the molecular basis of thermal tolerance, while building the technological feasibility for future ecological interventions deemed feasible and passing risk-benefit analysis.

5. TYPES OF 'REPAIR' INTERVENTIONS

5.1 Active restoration at reef-scale

Repair intervention types are implemented following disturbance and aim to facilitate recovery of impacted reefs. Reseeding of corals, for example, requires cost-effective propagation, production, and deployment of larvae, juvenile or adult stock of key species that, if restored, will provide an acceptable level of ecological function. Compared with prevention interventions, existing technologies in repair interventions have typically been small-scale (< 1ha) targeting local reefs. However, many large-scale prevention-intervention delivery methods build upon existing technologies of active restoration at the reef scale. These include direct transplantation, coral nursery production and micro-fragmentation, which have been extensively reviewed in report **T5—Current Practices** and will not be covered in great detail here (See **Box 7** for a summary).

Box 7: Current methods and technologies

Report **T5—Current Practices** details 329 case studies of coral-restoration projects that cover three intervention types: (1) recruitment and reproduction, (2) biocontrol, and (3) reef structures and stabilisation. Most case studies were from scientific literature (195), 79 were sourced from grey literature (i.e. reports and online descriptions), and 55 were responses to a global survey of restoration practitioners. Ten coral restoration intervention delivery methods are covered: coral gardening - transplantation phase (23 percent of records), coral gardening - nursery phase (17 percent), coral gardening (both phases, seven percent), direct transplantation (21 percent), substrate enhancement with electricity (four percent), larval enhancement (one percent), microfragmentation (less than one percent), substrate stabilisation (four percent), artificial reefs (19 percent) and algae removal (two percent). Most interventions involve coral fragmentation or transplantation of coral fragments (70 percent).

Practitioner-driven development has generated a series of production methods that use low-cost materials and are simple to deploy at small spatial scales. This has made active restoration techniques popular with lay-people, and projects often rely on an extensive volunteer labour-force. Active restoration delivery methods are therefore easily accessible, and can be deployed on local reefs, involving the local community. Thus, the potential for socio-economic benefits beyond purely ecological benefits are substantial (Hein *et al., 2019)*.

While many coral delivery methods have been developed, there is still a pauciy of data on the broader ecological outcomes of active restoration. Few projects have monitored long-term outcomes (median monitoring length is 12 months) and monitoring of metrics beyond the growth and survival of the transplanted corals remains rare (Hein *et al.,* 2017). Without appropriate monitoring, it is impossible to determine whether the significant time and economic investment in coral propagation is meeting ecological objectives. This mismatch between objectives and outcomes may also increase the risk of losing public trust by not delivering on project goals. Further, given that many active restoration techniques rely on harvesting wild coral colonies, there is a risk of overharvesting remnant healthy reef communities in order to replenish degraded areas. Finally, while it is evident that restoration without addressing the cause of disturbance is futile, few active restoration projects have incorporated climate change resilience, to date. Unless the ultimate cause of disturbance is mitigated, restored corals risk succumbing to the next mass-coral bleaching event.

The main messages from the report are:

1. On average, survival of restored corals is relatively high, at least in the short-term. All coral genera with sufficient replication from which to draw conclusions (more than 10 studies listing that genus) report an average survival between 60 and 70 percent.
2. Differences in survival and growth are largely species- and/or location-specific, so restoration methods should be tailored to the local conditions and to the specific objectives of each project.
3. Projects tend to be small and short. Substantial scaling-up is required for restoration to be useful in supporting the future survival of reefs. While there is ample evidence of successfully growing corals at small scales, few methods demonstrate a capacity to be scaled-up beyond 1ha. Notable exceptions include methods that propagate sexually

derived coral larvae. Long-term performance needs to be monitored.

4. To date, coral restoration has been plagued by the same common problems as restoration in other ecosystems. Mitigating these problems, outlined below, will be crucial to successfully scaling-up projects, and retaining public trust in restoration as a tool for resilience-based management.

    a. *Lack of clear objectives* - there are inconsistencies among the stated objectives of a project, the design of the project, and the monitoring of the project's outcomes. Poorly articulated or overinflated objectives risk alienating the general public, and scientists, by over-promising and under-delivering. Social and economic objectives have inherent value and do not need to be disguised with ecological objectives.

    b. *Lack of appropriate monitoring* - a large proportion of projects do not monitor metrics appropriate for their stated objectives, or do not monitor long enough to provide meaningful estimates of success. Further, there is a clear need for standardising the metrics used, to allow comparisons among projects.

    c. *Lack of appropriate reporting* - the outcomes of a large proportion of projects are not documented, which restricts knowledge-sharing and adaptive learning. While we attempted to access some of the unreported projects through our survey, it is clear we have only scratched the surface of existing knowledge.

    d. *Poorly designed projects* - some projects are inadequately designed and replicated in relation to for their specific contexts. Improved knowledge-sharing, capacity building and development of best-practice coral restoration guidelines will mitigate this problem.

See **T5—Current Practices** for more details.

5.1.1 Enhanced larval supply - sexual reproduction

Corals have a bipartite life history with a sessile (immobile) adult phase and a planktonic (mobile) larval phase during which they may be transported among reefs to establish new populations or replenish existing ones (Harrison, 2011; **Figure 14**). For most coral species, larvae are produced in annual mass-spawning events in which colonies release eggs and/or sperm (gametes) into the water column where fertilisation and subsequent embryogenesis occur, which results in the development of swimming planula larvae (Harrison, 2011). During mass-spawning events, the buoyant eggs can be so abundant they form conspicuous slicks on the ocean surface (Oliver and Willis, 1987). In other coral species, fertilisation and larval development occur inside the adult colony and the larvae are considered brooded (Harrison, 2011). Larvae can live for several months or more in the water column but are most capable of settlement relatively soon after release from the adult colony (Richmond, 1987; Wilson and Harrison, 1998). The process of settlement is an important stage in the lifecycle of corals as the choice of settlement site determines the coral's permanent location. Larvae use a range of physical and biological cues to inform this decision, to optimise the likelihood of survival (e.g. Baird *et al.*, 2003; Heyward and Negri, 1999). As settling corals are very small, they take one to two years to become visible to the naked eye (Babcock, 1991; Doropoulos *et al.*, 2016) and several additional years to grow large enough to become reproductively mature.

Following severe disturbances on reefs, many species rely on recruiting sexually derived larvae from other reefs to recover. Recruitment rates may be greatly reduced following bleaching (Hughes et al 2019). Several interventions seek to accelerate recovery by increasing the number of larvae or juveniles available for recruitment. Enhancing larval supply may be particularly desirable on reefs that receive a poor supply of larvae, either as a result of local hydrodynamics, or because widespread mortality has decimated source populations in the region (e.g. following a regional-scale bleaching event). The larvae used to repopulate reefs may improve recruit survival and can come from a variety of sources: endemic wild populations; translocated from other regions to accelerate gene flow; or sourced from cultured populations selected to express desirable traits such as heat tolerance. The method would likely be employed in conjunction with some form of engineered substrate.

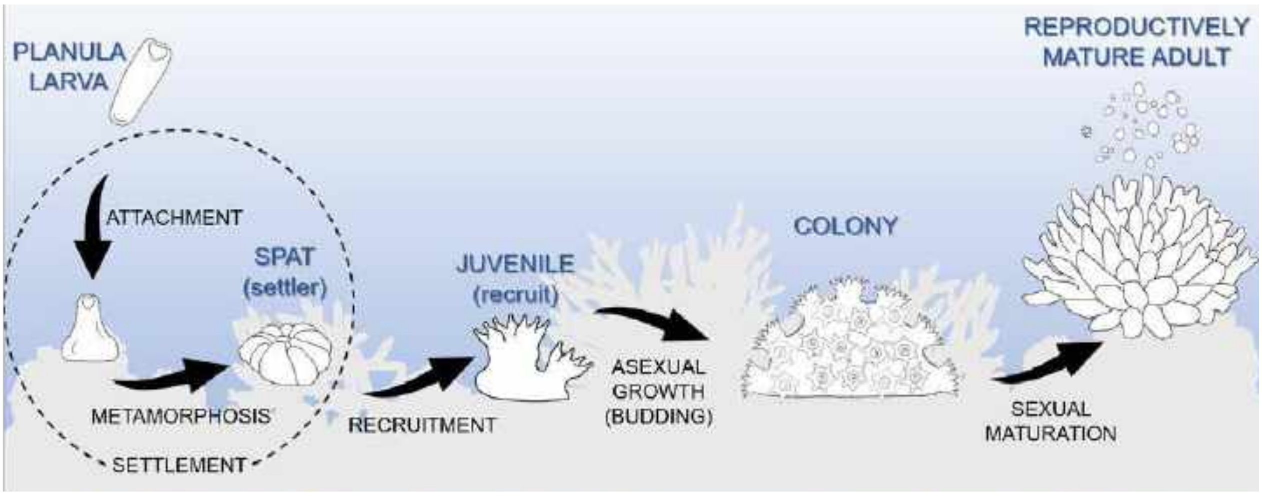


Figure 13: The bipartite lifecycle of corals includes a sessile (immobile) phase (from spat to reproductively mature adult) and a dispersive planktonic phase, which begins when gametes are spawned into the water column and continues through larval development, until larvae attach to the reef and metamorphose into spat in a process called settlement. Coral life-history stages are in blue, and processes are in black.

Enhancing recruitment onto reefs using sexually derived larvae (termed **larval seeding**) has been successfully trialled at small scales (10m^2). Most larval seeding trials have used larvae of single species (Guest *et al.*, 2014; Edwards *et al.*, 2015) spawned and reared in aquaria (e.g. Pollock *et al.*, 2017). Natural, wild slicks resulting from mass-spawning of corals (Oliver and Willis, 1987) have also been collected and reared using similar methods, before being pumped into fine mesh enclosures on reefs that are designed to prevent them from being dispersed (Heyward *et al.*, 2002; dela Cruz and Harrison, 2017). While enhanced settlement rates have been reported from larval seeding approaches, long-term (> 1 year) recruitment is not always higher than natural levels. Further, research is ongoing to test reproducibility and scale-up the method to larger areas (e.g. 100m^2; Harrison *et al.*, pers. comm.).

Larval seeding has the potential to be upscaled using commercial vessels designed to carry large volumes of seawater, and therefore large numbers of coral larvae (Doropoulos *et al.,* 2019). These larvae, whether sourced from natural slicks or industrial-scale aquaculture facilities, can be translocated over long distances to desired target reefs, where deployment could occur by either pumping larvae onto the reefs or deploying substrates that have newly-settled recruits (e.g. SECORE tetrapods or other substrata; Chamberland *et al.*, 2015, 2017; van Koningsveld *et al.*, 2017). At the reef-scale, large volumes of deployed larvae could reduce the cost per unit by not requiring enclosure in mesh cages upon deployment. Overall, the viability of these methods relies on low unit-cost, as the mortality of larvae and newly settled juveniles is high.

Harvesting natural slicks allows a diverse suite of species to be captured, leading to the re-establishment of reefs at a community level, rather than re-seeding a few select species, noting that some species do not spawn during mass-spawning events and others have negatively buoyant gametes and thus do not contribute to slick formation. Harvesting wild slicks is hypothesised to have a minimal effect on the source reef's ecology, as slick mortality is naturally high (through predation, dispersal failure, and post-settlement mortality). Harvesting natural slicks is expected to face minimal social and regulatory obstacles, particularly where it uses local populations as larval sources. Where translocation of slick-derived larave is involved, there are likely to be challenges around biosecurity, regulations, and social licence. Efficiently harvesting wild slicks would require: the improved ability to predict when and where slicks will form; a better understanding of natural survival rates within slicks; and improved understanding of the degree of species-bias within wild slicks.

5.2 Biological support to accelerate natural recovery

5.2.1 Substrate stabilisation and structure

Major disturbances such as severe cyclones can directly impact corals and damage the reef structure by destabilising coral rubble and reducing habitat complexity, which in turn, can increase the abundance of macro algae (Johns et al., 2018). Coral recovery may be reduced in such disturbed habitats because of low survival of coral juveniles in patches of loose rubble substrate and reduced settlement and post-settlement survival because of macroalgal competition (see **Section 5.2.3 Macroalgal removal**; Johns et al. 2018). The recovery of corals can also be inhibited by the loss of herbivorous fishes that can occur following the loss of habitat and structural complexity, which can influence local algal abundance. Intervention delivery methods that directly stabilise rubble or provide potentially cyclone-stable substrates that act as recruitment surfaces, can enhance rates of recovery of corals and reefs. Added structure can also provide habitat for herbivorous fishes, thus restoring a key ecological function. Rubble stabilisation methods also have the potential to enhance recreational diving and tourism at new or recovering sites by showcasing efforts to support recovery of degraded reefs. The functional benefits described above may be achieved through several delivery methods, explored in detail in the following sections.

Design of novel man-made structures

Substrate improvement to facilitate coral settlement and growth can occur by introducing artificial substrates, or by manipulating existing substrates across a range of spatial scales, from micro-scale engineered settlement surfaces to artificial reef structures. An artificial reef is a man-made structure that mimics one or more of the features that characterise a natural reef (Baine, 2001). By designing novel structures for settlement (e.g. new shapes, sizes and surfaces; e.g. Chamberland *et al.*, 2015, 2017) and large-scale structures (e.g. Subcon reef modules, ReefBall reef units, and Mars Reef Spiders), or using electrical current to stimulate mineral accretion (Goreau and Trench, 2013), new reef structures can aid both *in situ* and *ex situ* recruitment processes and enhance reef structural complexity.

There are many groups currently exploring the development and potential uses of novel substrate structures (e.g. BioRock, SECORE Project, Australian Institute of Marine Science SeaSim). The SECORE (SExual COral REproduction) Project has developed settlement tetrapods with grooves down the arms to promote coral settlement on artificial substrata in culture, and to maximise retention on the reef after deployment. The SECORE method, which allows corals to be placed on natural reefs with minimal handling, significantly reduces deployment and outplanting time of cultured corals, and reduces outplanting costs by up to 18-fold (Chamberland *et al.*, 2017; **Figure 15**), compared with directly adhering cultured corals to reefs. At larger scales, artificial reefs have been constructed of various materials to provide structure for coral settlement and reef function. Artificial reef structures range in size from clusters of reef balls (1-3m in diameter) to extensive areas of reef framework, created from quarried or dredged rock material at scales of hundreds of metres (Blakeway *et al.,* 2013). BioRock is a novel artificial substrate that uses low-voltage electrical current through steel structures to form solid limestone through underwater electrolysis (Goreau and Trench, 2013; **Figure 15**). SeaSim is currently testing the effects of substrate material, shape, aspect, and microcrevice structure, to maximise larval settlement across a diversity of species, and to enhance recruit and juvenile survival during the first 12 months.

In general, deployment at small scales would be diver or small-vessel-based, using passive or active placement of structures, with or without additional seeding of recruits or juveniles. Deployment methods would be site- or reef-specific and would require minimal time investments (days or weeks). At larger scales, artificial reefs would require industrial approaches to construction (Rio Tinto, 2015). Whether at small or large industry scale, the overall restoration effect would be still be at relatively small scales (tens to hundres of metres squared). The benefits would be experienced in years to decades, as outplanted corals grew and as others recruited through natural processes. Reef restoration outcomes could be enhanced by deploying artificial structures on high-value tourism sites, in conjunction with other interventions.

Regulatory permitting will range from low risk (substrate consolidation/stabilisation) to high risk (habitat engineering and artificial reefs), depending on the specific delivery methods used. Additional studies are required to determine optimum material types (e.g. anode metal in BioRock; Zamani *et al.*, 2010) or shape (e.g. tetrapod width; Chamberland *et al.*, 2015, 2017). At larger scales, the effects of artificial reefs on local water quality, flow dynamics and/or physical conditions, such as sediment dynamics, must be investigated.

Risks and indirect effects of novel substrata differ markedly, depending on the scale of intervention. When using novel surfaces and structures for outplanting cultured corals, the impact of the structures on the ecosystem are likely to be trivial, if constructed of inert calcium carbonate-based materials. At larger scales, construction of artificial reefs may be difficult to justify where natural reef substrata already exist. Potential negative effects to other reef organisms should be considered, including the potential shifts in community composition due to novel substrata favoring some species over others. Where hard substrata exist, novel substrata use is more likely to be through deployment of outplants. Coral survival on outplanted structures is predicted to be higher than natural survival rates. Therefore, this intervention has the potential to accelerate reef recovery, and promote tourism and recreational use of the Great Barrier Reef, at least at the local scale. Cost of large-scale reef construction (e.g. > $1km^2$) is likely to be much higher.

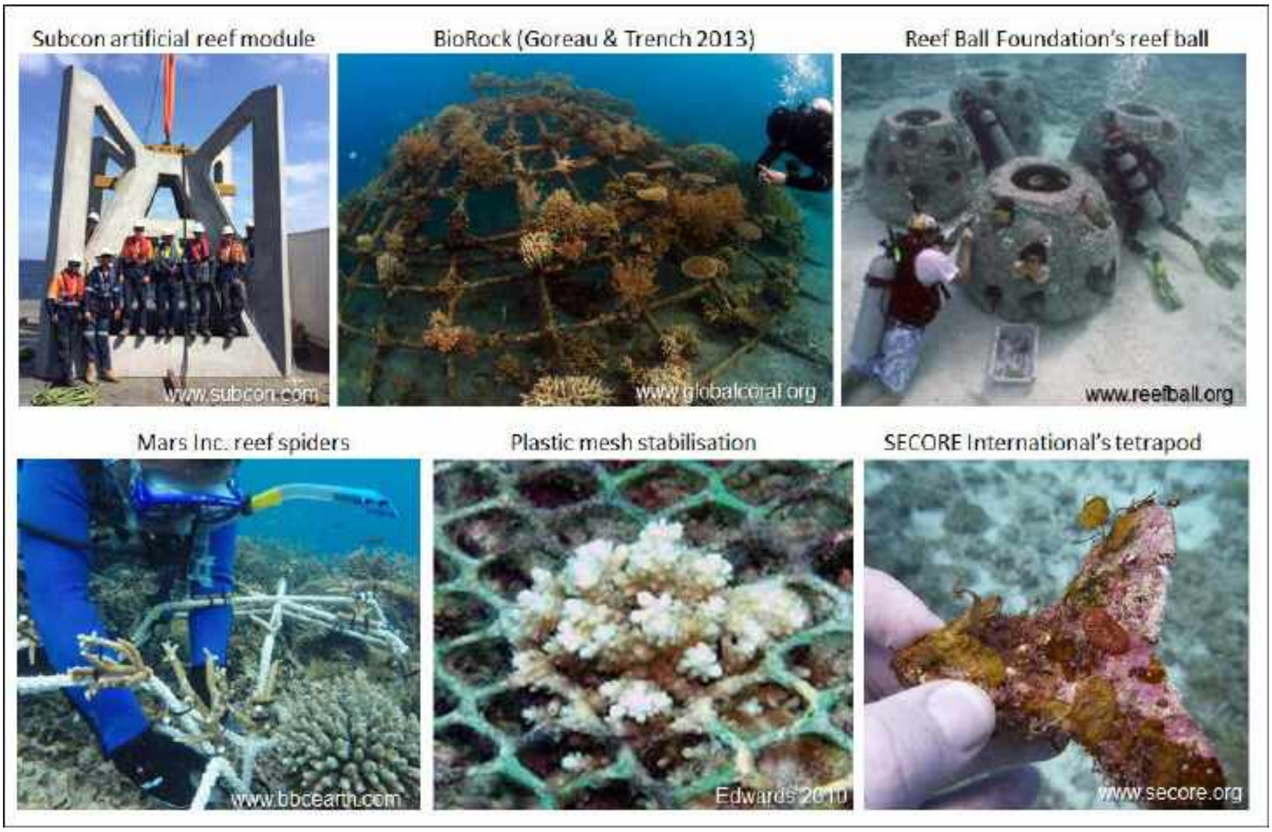


Figure 14: Example of artificial substrates and rubble stabilisation techniques from largest to smallest in scale.

Stabilisation of existing substrate

The physical restoration of damaged substrate has, until now, involved stabilising rubble over an area that has been damaged by acute disturbances such as storms or ship groundings. The rationale for such restorations is, on a damaged reef, corals cannot attach to loose substrata (Lindahl, 2003). While physical restoration has been relatively common in US territorial waters, funded by insurance claims following ship-strikes, there is a paucity of published literature that describes such methods. The most common technique is to install mesh or netting over the rubble to prevent further movement and encourage cementation processes. This is generally a precursor to transplanting corals or deploying artifical structures onto the damaged area (Lindahl, 2003). Other methods include driving metal reinforcement bars into loose substrate (Fox *et al.*, 2005), piling rocks on unstable degraded reef areas (Fox *et al.*, 2005), placing open cement structures that contain loose substrate onto damaged substrate (Hudson and Diaz, 1988; Clark and Edwards, 1995), and to inject grout or other chemicals to bond and stabilise loose rubble. Implementation of these approaches requires assessing the benefits of substrate stabilisation in the context of the natural level of consolidation on a particular reef. For example, on reefs that lack naturally consolidated substrata, rubble stabilisation may not be worth the risk and expense. Such stabilisation activities may, however, be beneficial on a small scale at high-value sites or following ship groundings that generate very large areas of unconsolidated rubble on naturally well consolidated reef framework (Great Barrier Reef Marine Park Authority, 2011).

Improvement of substratum settlement quality - microbiomes and CCA

Improvements to substratum quality for increased coral settlement and post-settlement survival can potentially be achieved by enhancing reef-associated benthic biofilms and/or crustose coralline algal (CCA) communities through the application of biological or chemical films to bare substrate. Ecological succession on reefs involves both positive and negative inter-species interactions, with the early colonisers of bare substrate able to modify the environment to make it more (i.e. inductive) or less (i.e. inhibitory) suitable for colonisation by other species arriving later in the successional process. Studies into ecological succession and post-settlement survival of corals generally define algae as the primary colonisers and coral as the secondary colonisers (Harrington *et al.*, 2004), with turf algae typically considered the earliest space occupiers and CCA considered mid successional colonisers (Birrell *et al.,* 2008). In addition, microorganisms also play an important role in the initial colonisation of bare surfaces, laying down exopolysaccharide and other chemical cues that modify the attractiveness of surfaces for subsequent colonisation by higher sessile organisms (Mieszkin *et al.,* 2013). Of particular relevance for the successful recruitment and post-settlement survival of corals are bacterial biofilms (Tran and Hadfield 2011, Hadfield 2011, Webster *et al*., 2004) which influence in a positive, neutral, or negative manner, the settlement of diverse micro and macro algae (Mieszkin *et al.,* 2013) which coral larvae may rely on for settlement and subsequently may outcompete settled recruits (Evensen et al., 2019; Johns *et al*., 2018). Appropriate surface films (biological or chemical) that control the successional trajectory of reef substrate to optimise coral settlement and post settlement survival could be applied under both aquaculture and field conditions. However, the optimal microbial community composition or chemical environment needed to support coral recruit survival is currently unknown and represents a key knowledge gap for application of this technology to restoration surfaces.

Introducing probiotic species to reef substrates is classified by the Great Barrier Reef Marine Park Authority as 'habitat engineering and artificial reefs', which is defined as high-risk. Deployment methods range from the introduction of priobiotic treatment capsules around restoration sites, the application of surface paints to reef structures and aquaculture enhancement of substrates prior to outplanting and could be combined with enhanced sexual larval supply. Maximum spatial scale effect of microbial substratum enhancement is predicted to be reefwide (> 10km^2) but it is unclear how long-lived the effects might be. While microbial enhancement has been shown to be beneficial *in vitro*, it remains to be tested whether it will result in significant recruitment enhancement *in situ*. Understanding and optimising successional processes at the scale of recruitment and post-settlement survival, are critical to the success of this intervention.

5.2.2 Coral health improvement

Corals obtain their nutrition from both **autotrophic** (i.e. from photosynthesis of microalgae) and **heterotrophic** (i.e. from externally captured food particles, such as plankton) processes. Manipulating the heterotrophic component of coral nutrition aims to increase survival, following environmental stress events that compromise their health. Supplementary nutrients, or alternative nutrients of higher quality, may help corals recover more quickly by helping restore impacted physiological functions such as growth, energy stores and reproduction. The impacts of environmental stress on coral physiology become particularly important during coral bleaching events, when endosymbionts are expelled, and corals experience decreased autotrophic capacity. Coral health could be restored with direct actions that aim to replenish energy stores that may in turn enable growth and reproduction (Conlan *et al.,* 2017).

Provide alternative foods to increase survival from stress

Lipids are a major source of energy storage in corals (Bergé and Bartnathan 2005) and can influence the outcome of bleaching events in individual coral colonies. Corals with higher quantities of lipids are more resilient to, and recover faster from, climate-change stressors (Rodrigues and Grottoli 2007, Baumann *et al.,* 2014, Towle *et al.,* 2015). Some coral species increase their heterotrophic feeding when bleached, to compensate for reduced autotrophic feeding, improving their chances of recovery (Grottoli *et al.,* 2006; Connolly *et al.,* 2012). Modelling of coral mortality from a bleaching event suggests that the timing between bleaching and mortality depends on the amount of lipids in store prior to bleaching, and heterotrophic capacity post-bleaching (Anthony et al 2009).

To date, most research into supplementing nutrients for corals has focused on the coral aquaculture process, primarily for the aquarium trade (Barton et al 2017). Additional feeding during vulnerable early lifestages could increase survival and growth (Conlan et al., 2017) and thus decrease time to a juvenile-size refuge, where survivorship increases substantially. For example, newly settled recruits of *F. fragum* and *A. tenuis* grew significantly faster—and had higher survival rates—when supplied with daily feeds of *Artemia salina* in an aquarium setting (Petersen et al 2008). Importantly, Toh et al (2014) demonstrated that benefits of feeding are evident even after transplantation to the reef. Colonies of *P. damicornis* that were fed with *A. salina* during their *ex situ* propagation phase, experienced higher growth rates and survival after transplantation to *in situ* coral nurseries. The authors calculated that feeding corals with high densities of nauplii decreased the cost of propagation 12-fold (Toh et al 2014). Further, alternative foods could potentially be packaged with probiotics, inoculated with symbionts or antioxidants (see section **5.2.2 Antioxidant/anti-microbial biological systems**).

In the context of increasing resilience to bleaching or other stressors, this delivery method has the most potential if deployed *in situ* prior to an expected bleaching event (to boost lipid stores in corals), and during the recovery stage (to increase capacity for heterotrophic feeding). Further research is needed to develop deployment methods *in situ*, the composition of manufactured feed to maximise recovery potential during a stress-event, finding the optimal nutrient balance, and exploring how species-specific potential benefits are.

Supplementing nutrients into the open reef system carries the potential of cascading risks associated with excess nutrients on reefs (D'Angelo and Wiedenmann 2014). Further, it is critical that the balance of nutrients is tailored to the coral algal symbiosis. Incorrect ratios of carbon, nitrogen and phosphorous can destabilise the symbiosis and make corals less resilient to thermal stress (Wiedenmann *et al.,* 2014; Morris *et al.,* 2019).

Antioxidant/anti-microbial biological systems

Higher disease prevalence has been correlated with the occurrence of warm seawater temperatures, potentially due to a decrease in immunocompetency of bleached corals (Maynard *et al.,* 2015). Therefore, removing coral disease and appying treatments (e.g. antioxidant/anti-microbial biological systems) could help mitigate coral diseases (stopping the spread and/or limit the effects), and may contribute to the recovery of bleached corals. Mitigation and diagnostics of coral diseases with microbial interventions is currently limited, as most of the disease aetiologies are not fully understood (Pollock *et al.,* 2011). This leads to immunisation treatments that are difficult to apply in environmental scenarios. Current successful strategies to mitigate coral disease are very localised and include the direct application of underwater epoxy to prevent black band disease on corals from spreading, as well as surgically removing affected tissue

(Raymundo *et al.,* 2008). These direct techniques can be very effective, reducing tissue loss by up to 30 percent in treated corals (Aeby *et al.,* 2015). However, this approach is very labour intensive and impractical over large areas.

Innovative strategies have shown promising results, such as **phage therapy**, which is the treatment of a bacterial disease with a virus. Phage therapy is a promising alternative to antibiotics. It has been successfully applied in aquaculture to mitigate bacterial pathogens in several species, such as catfish (*Clarias batrachusm*), ayu fish (*Plecoglossus altivelis*) and shrimp (*Penaeus monodon*; Oliveira *et al.,* 2012). Also, coral bacterial pathogens have been treated through phage therapy, such as *Vibrio coralliilyticus* (Efrony *et al.,* 2007, 2009; Atad *et al.,* 2012; Cohen *et al.,* 2013) and *Thalassomonas loyana* (Efrony *et al.,* 2007, 2009). Phage therapy has been successfully used to control *T. loyana*, a bacterium that can cause white plague-like disease in the coral *Favia favus* (Thompson *et al.,* 2006). Treatment inhibited the progression and transmission of white plague-like disease to neighbouring corals in both a laboratory experiment (Efrony *et al.,* 2007) and a seven-week field trial in the Red Sea (Atad *et al.,* 2012). The logistics associated with large-scale applications of phage therapy on coral reefs have not been studied thoroughly enough to be considered for large-scale applications in the Great Barrier Reef. A better understanding of feasible coral disease mitigation strategies is required, including a better understanding of disease etiology, the establishment of a robust coral disease diagnostic system (Pollock *et al.*, 2011) and the development of practical and safe delivery methods that can be scaled.

Given the importance of microbial relationships on the Reef, any intervention that aims to disrupt deleterious (i.e. disease-causing) relationships, runs the risk of unintentionally affecting unrelated microbes. For example, manual treatment of coral disease has the potential for further disease transmission through infected tools and other equipment. Phage therapy releases a virus which has the capacity to self-replicate and evolve, potentially spreading uncontrollably throughout an ecosystem. Once introduced into the open reef ecosystem, it would be virtually impossible to control or remove.

5.2.3 Biocontrol

Interventions that aim to control crown-of-thorns starfish are already implemented, particularly on high-value tourism sites on the Great Barrier Reef. These interventions could potentially be extended to other predatory or competing species that are reducing coral cover or impeding recovery following a disturbance. This report only addresses the removal of macroalgae and *Drupella* spp. (a predatory snail). For more information on crown-of-thorns starfish the reader is directed to Westcott *et al.,* (2016).

Macroalgal removal

Macroalgae occur naturally in coral reef ecosystems (Fulton *et al.*, 2016). Yet, when the ecosystem is under pressure, macroalgae can become so abundant they overgrow corals, prevent settlement, and outcompete recruits, which can cause phase shifts from coral to macroalgal domination (Marimuthu *et al.*, 2016; Ceccarelli *et al.*, 2018). Phase shifts from coral to algal-dominated states have been recorded primarily on Caribbean reefs (e.g. Hughes 1994; Mumby 2009), although general declines in coral cover and corresponding increases in macroalgal cover have been reported on the Great Barrier Reef (Hatcher, 1984; Done, 1992; Done *et al.*, 2007; Diaz-Pulido *et al.*, 2009; Cheal *et al.*, 2010; De'ath *et al.*, 2012). Macroalgae have the potential to negatively affect corals directly and indirectly through shading, space occupation, abrasion, pathogen transmission, chemical inhibition, and fueling detrimental microbial pathways (Birrell *et al.*, 2008; Morrow *et al.*, 2011; Vega Thurber *et al.*, 2012). Specifically, macroalgae can reduce coral **fecundity** (Cetz-Navarro *et al.*, 2015), inhibit larval recruitment and **metamorphosis** (Baird and Morse, 2004; Webster *et al.*, 2015), and reduce juvenile growth and survival (Hughes *et al.*, 2007, Webster *et al.*, 2015). Macroalgae reduced survival of nursery-reared *Acropora* coral (van Woesik *et al.*, 2017) and growth and fecundity of *Acropora* coral was significantly higher when macroalgae was cleared (Tanner, 1995).

Macroalgae removal aims to enhance coral survival, growth, and recovery in areas where competition for space exists. Manual removal of macroalgae is labour-intensive. When conducted by a diver, it can be completed by hand or with tools to facilitate removal (e.g. scraper, suction device). For enhanced and longer-term results (months to years), macroalgal holdfasts must be fully removed (Loffler and Hoey, 2017). Biologically-assisted macroalgal removal, such as herbivory by urchins (Stimson *et al.*, 2007; Barlow *et al.*, 2010; Idjadi *et al.*, 2010) herbivorous fishes (Trapon *et al.*, 2013), and crustaceans (Spadaro 2014) present the greatest potential for long-term management of macroalgae and enhancement of coral recruitment on coral reefs, as manual removal by divers requires regular maintenance to suppress regrowth (Hancock *et al.*, 2017).

The potential costs, benefits and risks of active removal of macroalgae for coral reef restoration are largely unknown (Tanner, 1995; van Woesik *et al.*, 2017). Macroalgae occur naturally and, on healthy reefs, have positive effects on coral reef ecosystems; hence, their removal presents ecological risks. Macroalgae removal could influence local biodiversity by limiting food and habitat, as well as reducing recruitment of fish larvae (Wilson *et al.*, 2010; Evans *et al.*, 2014; Radulovich *et al.*, 2015; Streit *et al.*, 2015). (Box 7).

Box 8: Is removing macroalgae a good idea?

Ceccarelli *et al.,* 2018 reviewed the available literature regarding positive and negative ecosystem effects of macroalgae, and how macroalgae removal may affect the ecosystem. Excerpts below are from the main conclusions of the review paper reproduced here with permission from the author.

Despite the documented deleterious effects of macroalgae on coral populations, there is very little literature documenting macroalgae removal as a tool for reef restoration. Algae removal is sometimes conducted as part of the maintenance regime in coral transplantation projects, but is rarely quantified (Shaish *et al.,* 2010; Forrester *et al.,* 2012; Frias-Torres & van de Geer, 2015). Eight case studies across the Caribbean, Indian and Pacific Oceans illustrate the potential successes and failures of macroalgae removal. Removal was conducted by divers, either entirely by hand or assisted with hand tools and/or a suction device.

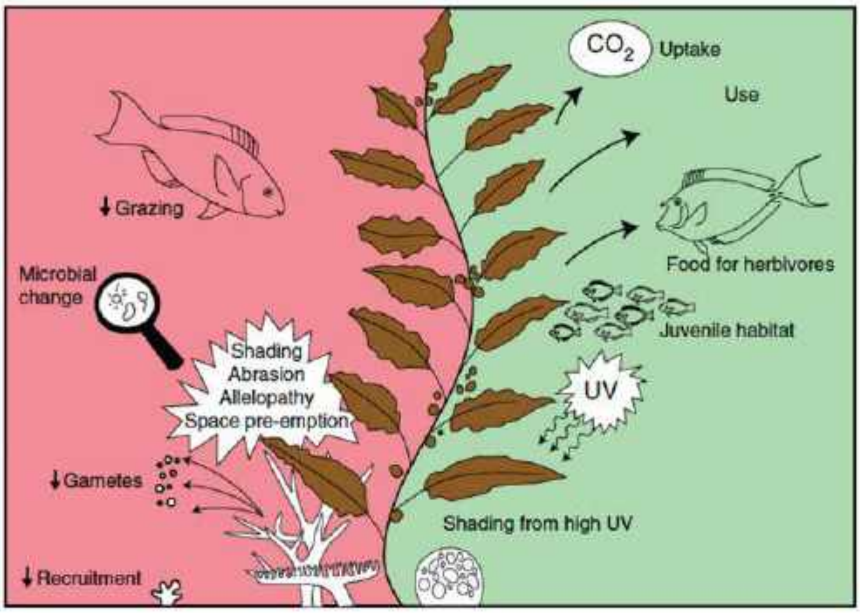
Two important insights were gained from the case studies:

- Combined enhanced herbivory and active algae removal was optimal (Hancock *et al.,* 2017).
- It is necessary to remove the anchoring holdfast to prevent immediate regrowth (Loffler & Hoey 2017).

Very little data exist to support an evaluation of the long-term success of macroalgae removal as a reef restoration technique. Given the widely reported negative effects of increasing macroalgal cover or biomass on coral reefs generally, the expectation of a positive effect on the settlement and growth of corals appears reasonable (van Woesik *et al.,* 2017). The following considerations should guide the evaluation of algae removal as a management tool:

1. **Establishing the need for removal by demonstrating a phase shift or 'threshold' abundance of macroalgae:** the macroalgal abundance level that should trigger intervention will vary by site. Ideally, this threshold would be based on temporal changes in macroalgal abundance and corresponding declines in coral juvenile abundance and/or adult coral cover, but in many instances such data do not exist. In an ideal scenario, macroalgal biomass would be reduced to levels prior to the increase.
2. **Interaction with herbivory:** Previous studies suggest the most successful removal efforts were coupled with an introduction of herbivores if their density is low (Hancock et al. 2017). Re-introducing or protecting herbivores prior to algal removal can allow the herbivores to establish control by consuming new plants and prevent regrowth of existing ones. With effective protection, herbivore populations can recover rapidly and reach unfished biomass within a year (Mumby et al. 2006).
3. **Methods and logistics:** Macroalgal reduction is usually undertaken by hand, with or without scrapers or suction devices. Information is needed on the optimal size of cleared patches, and the frequency of macroalgal reduction. Removal during the early growing season may be more effective than late in the growth period. The success of removal methods will depend on biological characteristics that vary extensively among algal morphs and species.
4. **Potential negative effects of macroalgae removal***:* Removal of algal holdfasts may disturb or damage the substrate and may injure corals and other benthic

organisms. For example, *Sargassum* spp. generally negatively impact coral (e.g. shade, space domination, abrasion, hostile allelochemistry), but their removal may open space for the potentially more detrimental ephemeral algae, which, despite its short-lived nature, can form dense carpets that deplete oxygen and kill or stress the benthos. Removing plant biomass and physical structure may result in declines in other taxa such as fishes—especially species that recruit into stands of macroalgae—and affect microbial, physical, and chemical parameters. These risks should be assessed prior to large-scale macroalgae removal on coral reefs.



Conceptual diagram summarising positive (green) and negative (red) effects of fleshy macroalgae on coral reefs. Reproduced from Ceccarrelli *et al.,* 2018

5. **Response of corals to macroalgae removal and controlling chronic stressors:** Following algal removal many factors likely to affect the recruitment, growth and survival of corals include connectivity to larval sources, the quality of the receiving environment, the availability of suitable settlement substratum, and other natural and anthropogenic drivers of coral communities. The success of removal projects may be enhanced by simultaneous interventions to enhance coral recruitment. It will also depend on controlling chronic stressors.
6. **Measures of success:** The performance indicators for restoration success should be clearly defined and measured with standard scientific principles[1] (McDonald *et al.,* 2016). Local management teams may begin with short-term, small-scale goals, scaling up measures of success as a restoration program expands. Hein *et al.,* (2017) proposed 10 socioecological indicators of reef restoration success: coral

[1] Common to all interventions not just macroalgal removal.

diversity, herbivore biomass and diversity, benthic cover, recruitment, coral health, reef structural complexity, reef-user satisfaction, stewardship, capacity building, economic value. Immediate, short-term and long-term measures of success need to be considered in the sampling design. The measure of success for a macroalgae reduction program should ultimately be whether coral and algal cover have returned to baseline pre-disturbance levels, and whether the remaining macroalgal beds are fulfilling the role of nursery, habitat and food for dependent species.

Drupella management

In certain circumstances predation by species other than crown-of-thorns starfish may negatively impact coral cover and recovery from disturbance. Coral-eating snails of the genus *Drupella* can cause significant coral mortality at local scales and on remnant populations following impacts (e.g. Cros and McClanahan 2003; Bruckner *et al.*, 2017). Collection and removal of coral-eating snails by hand to protect corals has been shown to be effective at limited spatial and temporal scales (Miller, 2001; Williams *et al.*, 2014). Further, manual removal of a common Caribbean coral-eating snail (*Coralliophila abbreviata*) increased the resistance and recovery of treated corals (*Pseudodiploria* and *Diploria* spp.) to bleaching (Shaver *et al.,* 2018).

Push-pull technologies use pheromones or other chemical signals to disperse or aggregate pest species as part of integrated pest-control strategies. ‘Push’ technologies (in development for crown-of-thorns starfish), release chemicals from natural predators, which may elicit a strong escape response in the target species (e.g. Paterson, 1990; Hall *et al.*, 2017). If such compounds were characterised and synthesised for coral predators such as *Drupella* snails, they could potentially be deployed in high-value coral reef areas to reduce predation. A risk of push technologies is that they may disperse predators rather than reducing their population levels. In contrast, pull-technologies draw in the target species so that they can be trapped and more cost-effectively removed. Potential pull technologies could be based on feeding, sexual or other aggregative pheromones (Kita *et al.*, 2005). The spatial and temporal scales at which push-pull technologies could be deployed are presently limited to sites, and time scales of months. Application at larger scales will require innovation in deployment such as biodegradable, single-use, slow-release units.

Risks include potentially disrupting the biology and ecology of other species, and currently little is known about how push-pull technologies may interfere with other reef species. Developing species-specific technologies may be necessary, particularly for pheromone-based pull techniques. Further research and development are required to determine if *Drupella* predation is a problem and to quantify the benefits and risks of push-pull technologies.

Biological control of *Drupella* by natural predators offers an alternative approach to protect high-value corals (e.g. Cros and McClanahan 2003; Bruckner *et al.*, 2017). Modelling indicates that abundant predator populations such as mutualistic crabs that inhabit corals (McKeon and Moore, 2014; Samsuri *et al.*, 2018) could provide effective control of *Drupella* populations (Ratianasingh *et al.*, 2017). Therefore, outplanting restored corals with biological control organisms could protect corals from predation but will need to account for crab/coral-host specificity and an ability to be bred in captivity. Assuming no major barriers to breeding, small-scale deployment of crabs combined with manual removal or trapping of *Drupella* may be feasibile.

If methods of biological control prove to be effective in reducing coral mortality, they could be combined with transplantation-based interventions to ensure post-deplyment success. Risks from stocking cultured crabs include introducing disease and biosecurity and would need to be carefully controlled. Ecological risks to other reef fauna would need to be examined.

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APPENDIX A – RRAP DOCUMENT MAP

APPENDIX B – GLOSSARY

All relevant terms are in **BOLD PURPLE** throughout this report.

(Physiological) acclimatisation - (i) phenotypic changes by an organism (usually reversible and limited by the genotype) to stressors in the natural environment that result in re-adjustment of the organism's tolerance levels (Coles and Brown, 2003); (ii) (phenotypic plasticity) the capacity of an organism to tune its biochemical attributes and physiological performance to a variety of environmental conditions within its lifetime and is also referred to as phenotypic plasticity (Coles and Brown, 2003; Weis, 2010; Brown and Cossins, 2011; Sanford and Kelly, 2011); (iii) the ability of the same genotype to adjust its phenotype under different environmental conditions without genetic change (reversible, developmental or transgenerational; Webster and Reusch, 2017).

(Developmental) acclimatisation - irreversible phenotypic plasticity resulting from environmental cues experienced during development (also known as developmental plasticity; Munday *et al.*, 2013).

(Transgenerational) acclimatisation (TGP)) - acclimatisation or plasticity passed between generations potentially through epigenetic programing or vertically transferred microbial communities; (ii) the phenotype of a new generation is influenced by the environment experienced by the previous generation (Torda *et al.*, 2017).

Adult (coral) - mature coral colony, capable of sexual reproduction, through internal brooding of larvae or broadcast spawning and subsequent external fertilisation.

Albedo – a measure of how much light hits a surface and is reflected without being absorbed. Something that appears white reflects most of the light that hits it and has a high **albedo**, while something that looks dark absorbs most of the light that hits it, indicating a low **albedo.**

Allele – a variant form of a gene. Some genes have a variety of different forms, which are located at the same position, or genetic locus, on a chromosome. Humans are considered diploid organisms because they have two **alleles** at each genetic locus, with one **allele** inherited from each parent.

Amplified fragment length polymorphism (AFLP) - fragments of DNA (50-500bp) used in DNA fingerprinting.

Assisted evolution (AE) - the acceleration of naturally-occurring evolutionary processes via human intervention to enhance certain traits (Jones and Monaco, 2009; van Oppen *et al.*, 2015); holistic term that includes genetic adaptation, transgenerational changes through epigenetic mechanisms, and modifications in the community composition of microbes associated with the target organism (van Oppen *et al.*, 2017).

Assisted gene flow (AGF) - (i) intentional translocation of individuals within a species range to facilitate adaptation to anticipated local conditions (Aitken and Whitlock, 2013); (ii) managed movement of individuals into populations to reduce local mis-adaptation to climate or other environmental changes (Whiteley *et al.*, 2015).

Assisted colonisation - the intentional movement of focal units (ecotypes, species, taxa, functional types, life forms) to recipient localities, where these focal units are currently absent, and where they cannot be expected to colonise by natural means within a short time (i.e. years or decades; Kreyling *et al.*, 2011).

Assisted migration - intentional translocation of individuals within or outside the natural range of a species (Aitken and Whitlock, 2013).

Autotroph – an organism capable of synthesising its own food from inorganic substances, using light or chemical energy. Green plants, algae, and certain bacteria are autotrophs.

Beneficial microorganisms for corals (BMC) - coral symbionts that possess potential beneficial traits, including nutritional ('probiotics') and protective mechanisms that improve coral fitness and contribute to coral resilience (Peixoto *et al.*, 2017).

Biofilm - a complex assemblage of microorganisms, including bacteria, diatoms, fungi, protozoa, other small organisms, and can also include a large amount of secreted extracellular polymeric substance in which the cells of the component organisms are buried (Hadfield, 2011).

Cells – the cell is the basic structural, functional, and biological unit of all known living organisms. A **somatic cell** is any biological cell forming the body of an organism other than a gamete, germ cell, gametocyte or undifferentiated stem cell. The **germ line** are cells that give rise to gametes of organisms that reproduce sexually.

Co-adapted gene complexes – specific combinations of genes at multiple loci that interact to confer higher fitness relative to other genotypes.

Colony - term to describe any coral that has two or more genetically identical polyps. Usually reserved for larger, easily visible coral colonies.

Conditioning - inducing a shift in the phenotypic performance of an organism due to sub-lethal stress exposure.

CRISPR/Cas9 genome editing - originally isolated from 'Clustered Regularly Interspaced Short Palindromic Repeats' acquired immune systems in bacteria, Cas9 is a non-repetitive enzyme that can be directed to cut almost any DNA sequence by simply using a 'guide RNA' containing that same sequence.

Delivery method - The method to deploy the intervention. Delivery methods consist of three parts: the specific approach, production, and deployment on the Reef. The same production and deployment methods may be combined with different approaches to deliver different interventions. For example, aquaculture production can enhance recovery or adaptation depending on the stock and treatments used.

Environmental adjustment - reef-scale physical implementations to reduce the exposure of corals to acute environmental stress events.

Epigenetics - (i) the external modification of genes (without a change in the actual gene sequence) that causes a change in expression level of those genes (i.e. DNA methylation, histone tail modification, chromatin remodelling and biogenesis of small non-coding RNAs; Handel *et al*., 2010); (ii) regarding turning genes on or off, stable cellular memory that persists after cell division, and, in some cases, even through sexual reproduction (Crossley, 2013); (iii) a term originally coined by Waddington in 1940, intended to explain the phenomenon of cellular differentiation in multicellular organisms from a single genome, and more recently the concept has evolved to include all mechanisms that potentially regulate gene expression (i.e. DNA methylation, histone modifications and variants, noncoding and antisense RNA; Torda *et al.,* 2017); (iv) environmentally induced changes not encoded in the base sequence of the DNA that may nevertheless alter gene expression levels and have a heritable component (i.e. DNA-methylation marks, histone acetylation and microRNA; Webster and Reusch, 2017).

Epistasis - the interaction of genes that are not alleles, particularly the suppression of the effect of one such gene by another.

Experimental evolution - the directed evolution of a population across multiple generations under *defined* and reproducible conditions (generally in a laboratory; FAO report, 2017).

F1 – an F1 hybrid is the first filial generation of offspring of distinctly different parental types. F1 hybrids are used in genetics, and selective breeding. Subsequent generations are called F2, F3 and so on.

Facilitated adaptation - (i) rescuing a target population or species by endowing it with adaptive alleles, or gene variants, using genetic engineering (Thomas *et al*., 2013); (ii) supplementing genomic diversity of bottle-neck populations to increase adaptive potential in a changing environment (Johnson *et al*., 2016).

Fecundity – a term used in demography and population biology to describe the potential for reproduction of an organism or population, measured by the number of gametes (eggs), seed set, or asexual propagules.

Functional diversity - a component of biodiversity that generally concerns the range of things that organisms do (functions) in communities and ecosystems.

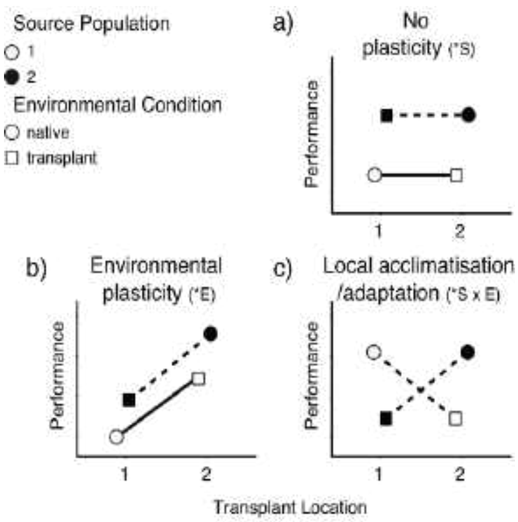
Functional objective - the core benefit being targeted by an intervention, such as reducing conditions that induce bleaching, or enhancing the ability of Reef populations to recover from, or withstand, bleaching.

Functional objective type - Groupings of like functional objectives used to cluster interventions that share intended benefits, such as reducing conditions that induce bleaching, or enhancing the ability of Reef populations to recover from, or withstand, bleaching. They have been used for communication and outreach purposes as they commonly have similar social and regulatory considerations.

Gene drive - (i) technique for spreading selected, usually recombinant, DNA sequences (genes) through wild populations with the aim of eliminating unwanted characteristics of an organism or adding desired characteristics (Piaggio *et al.*, 2017); (ii) a stretch of DNA that is inherited more frequently than normal. In sexually reproducing organisms, most DNA sequences have a 50 percent chance of being inherited by each offspring ('Mendelian inheritance'), while gene drives manage to rig the system so that they are inherited more frequently (up to 100 percent of the time; Esvelt website: http://www.sculptingevolution.org/genedrives/genedrivefaq).

Gene swamping - rapid increase in frequency of an introduced variant that leads to substantial replacement of local variants due to a numerical or fitness advantage (Hufford and Mazer, 2003).

Genotype by environment interaction - (i) two different genotypes respond to environmental variation in different ways; (ii) potential phenotypic responses revealed by a reciprocal transplant design: (a) fixed differences in the performance of corals from different source populations regardless of environmental exposure (source effect), indicating no plasticity in phenotypic responses; (b) plasticity in the performance of corals depending on the environment (environmental effect), leading to similarly expressed phenotypes at a given location and acclimatisation of foreign genotypes to local conditions; and (c) a source by environment interaction, indicating local adaptation arising from genetic effects or potentially through developmental canalisation (Rocker, 2016).



(Genetic) adaptation - a change in phenotype from one generation to the next through natural selection and involves a genetic change in the form of allele frequency changes between generations; (ii) when the more stenotopic members of a population are eliminated by environmental stress, leaving the more tolerant organisms to reproduce and recruit to available habitat (Coles and Brown, 2003); (iii) the fine-tuning of populations to their local environment via natural selection, resulting in resident genotypes with a higher fitness in their native habitat than foreign genotypes from more distant populations (Sandford and Kelly, 2011).

Genetic engineering (modification/manipulation) - the development and application of technologies that permit direct manipulation of genetic material to alter hereditary traits of a cell or organism (Piaggio *et al.*, 2017).

Heterosis (hybrid vigour) - (i) an increase in fitness relative to parental populations; (ii) 'the physiological vigor' of a heterozygous offspring in terms of growth, height and general robustness compared with its parents (Shull, 1948).

Heterotroph – an organism that cannot manufacture its own food by carbon fixation and therefore derives its intake of nutrition from other sources of organic carbon, mainly plant or animal matter. In the food chain, heterotrophs are secondary and tertiary consumers.

Holobiont (coral) - the collective community of the coral host and a range of eukaryotic and prokaryotic microorganisms (Rohwer *et al.*, 2002; Ainsworth *et al.*, 2010).

Hybridisation - interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations (Rhymer and Simberloff, 1996).

Intervention (under RRAP) - suite of tools that can be deployed for large-scale restoration and adaptation.

Introgression - (i) new alleles entering the population by hybridisation with members of a differentiated population or even a different species (Ellegren and Galtier, 2016); (ii) the permanent incorporation of genes from one differentiated population to another (Petit and Excoffier, 2009); (iii) gene flow between populations whose individuals hybridise, achieved when hybrids backcross to one or both parental populations (Rhymer and Simberloff, 1996).

Juvenile (coral) - Sexually immature coral that has grown from a spat into a juvenile through the process of asexual budding. Often used interchangeably with 'recruit'. Generally, 'settlers' are younger than 'recruits', which are younger than 'juveniles'.

Larval (coral) - Planktonic stage of a stony coral, also called a planula. Larvae develop through the process of embryogenesis & larval development.

Larval seeding - enhancement of recruitment onto reefs using sexually derived larvae.

Local adaptation - higher fitness of local than nonlocal populations resulting from divergent selection among environments (Aitken and Whitlock, 2013).

Loci - a locus (plural loci) is a fixed position on a chromosome, or any region of genomic DNA, that is considered to be a discrete genetic unit. It can range in length from a few base pairs to a megabase-size region containing a large gene family (Silver 2001).

Marine cloud brightening (MCB) - a method of mitigating bleaching of corals by increasing the reflectivity (also known as albedo) of low-lying marine clouds over the reef so that they reflect more of the sun's incoming solar radiation back into space (Harrison, 2018).

Metamorphosis - a biological process by which an animal physically develops. It involves a conspicuous and relatively abrupt change in the animal's body structure through cell growth and differentiation. For corals, metamorphosis marks the transition from larva to spat.

Microbe – A microorganism, or microbe, is a microscopic organism, which may exist in its single-celled form or in a colony of cells. Microorganisms include all unicellular organisms and so are extremely diverse. All archaea and bacteria are microorganisms and were previously grouped together as prokaryotes. The third domain, Eukaryota, includes all multicellular organisms and many unicellular protists and protozoans.

Microbiome (coral) - (i) the collective genome of the coral-associated (symbiotic and non-symbiotic) microorganisms (Ainsworth *et al.*, 2010); (ii) the collective genome of micro-organisms or microbial assemblages (bacteria, archaea, protists) associated with any system such as the body of an animal, a water or soil sample, or an entire ocean (Ainsworth *et al.*, 2010); (iii) the sum of genetic information of the microbiota (Rosenberg *et al.*, 2016); (iv) the entire microbial community (and associated genes) that resides on or within a coral (Bourne *et al.*, 2016).

Microbiome-mediated transgenerational acclimatisation (MMTA) - because rapidly dividing microbial species can evolve much faster than the host, adaptive evolution can occur within weeks to months (Elena and Lenski, 2003), which is two to three orders of magnitude faster than genetic adaptation at the population level for the coral hosts (Webster and Reusch 2017). If this acclimatisation is vertically transmitted it would enable microbiome-mediated transgenerational acclimatisation (MMTA) of reef species.

Mutagenesis - the change of genetic information resulting in a mutation that may be spontaneous in nature, due to mutagen exposure, or experimentally induced in the laboratory.

National Environmental Research Program (NESP) - a long-term commitment by the Australian Government to environment and climate research; projects deliver collaborative, practical and applied research to inform decision making and on-ground action.

Natural selection - the process whereby organisms better adapted to their environment tend to survive and produce more offspring. The theory of its action was first fully expounded by Charles Darwin, and it is now regarded to be the principal process that brings about evolution. The death, or non-reproduction, needed for selection may be hard or soft.

Hard natural selection - occurs when one gene or variant is substituted completely for another. This may occur by means of an extreme advantage of one gene over another resulting in decreased fitness and subsequently increased mortality of individuals within a population with those genes or variants.

Soft natural selection – occurs when genes or variants are substituted at varying proportions throughout a population due to differential fitness of individuals. This may cause shifts in genes or variants within the population without an increase in the background mortality rate.

Ocean Thermal Energy Conversion (OTEC) - a process that can produce electricity by using the temperature difference between deep cold ocean water and warm tropical surface waters.

Outbreeding depression - (i) loss of fitness resulting from intra- or interspecific hybridisation caused by the disruption of either intrinsic gene interactions (epistasis) or interactions of genes and environment (Baums, 2008); (ii) lowered fitness in offspring, or later generations, of crosses between genetically different sources (Rhymer and Simberloff, 1996); (iii) a threat to small populations as it reduces the reproductive capacity of the population through demographic swamping, thus increasing the probability of population extinction (Byrne *et al.*, 2011); (iv) reduction in mean population fitness resulting from hybridisation between genetically distinct individuals or populations of the same species (detected in F1 or subsequent generations; Hufford and Mazer, 2003).

Outplanting - attaching nursery-grown fragments to natural or engineered substrate using epoxy, cement, or cable ties.

Phage therapy - treatment of bacterial disease with a virus.

Phenotype - the composite of an organism's observable characteristics or traits, including its morphology or physical form and structure; its developmental processes; its biochemical and physiological properties and its behaviour. The phenotype results from the expression of the genetic code, or its genotype, and the influence of environmental factors. The genotype and environment may also interact, further affecting phenotype.

Prevention (under RRAP) - technologies and processes to reduce exposure to, and impacts of, disturbance.

Probiotics - (i) live microorganisms that, when administered in adequate amounts, confer a health benefit to the host (FAO/WHO, 2002); (ii) for increasing coral resilience this will likely include bateria, the algal endosymbionts and/or fungi (FAO report, 2017); (iii) a live microbial feed supplement that beneficially affects the host animal by improving its intestinal balance (Fuller, 1989; Peixoto *et al.*, 2017)

Quantitative trait locus (QTL) - a section of DNA (the locus) which correlates with variation in a phenotype (the quantitative trait) and are mapped by identifying molecular markers (such as SNPs or AFLPs) that correlate with an observed trait.

Recruit (coral) - Newly ‘settled’ coral of the benthic polyp stage. Term is usually reserved to describe corals of one or a few polyps only. Often used interchangeably with ‘spat’ and ‘settler’.

Repair (treatment; under RRAP) - technologies and processes to enhance recovery after disturbance (e.g. coral bleaching, crown-of-thorns starfish outbreaks, cyclones, or ship groundings).

Reverse genetics - method to help understand the function of a gene by analysing the phenotypic effects of specific engineered gene sequences (Cleves *et al.*, 2018).

(Environmental) shading - conditions that decrease solar irradiance (e.g. cloud cover, high turbidity) and offer protection to corals under thermal stress (Coelho *et al.*, 2017).

Settler (coral) - Newly 'settled' coral of the benthic polyp stage. Term is usually reserved to describe corals of one or a few polyps. Often used interchangeably with '**spat** and '**recruit**'.

SNP (single nucleotide polymorphism) - the most common type of genetic variation represented by a difference in a single nucleotide.

Spat (coral) - Newly 'settled' coral of the benthic polyp stage. Term is usually reserved to describe corals of one or a few polyps. Often used interchangeably with '**settler**' and '**recruit**'.

Stress hardening - a process where prior exposure to stress events (e.g. extreme heat or cold) increases the tolerance to successive events.

Synthetic biology - (i) emerging area of research that can broadly be described as the design and construction of novel artificial biological pathways, organisms or devices, or the redesign of existing natural biological systems; (ii) the application of science, technology, and engineering to facilitate and accelerate the design, manufacture and/or modification of genetic materials in living organisms (SCENIHR *et al.*, 2014; Piaggio *et al.*, 2017).

Transgressive hybridisation - the creation of hybrids with phenotypes more extreme than their parental lines (Whiteley *et al.,* 2015).

Vertical mixing - in the oceans, an upward and downward movement of water that occurs as a result of the temperature gradients (temperature differences between layers of the fluid).

Reef Restoration and Adaptation Program

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